Testing the social complexity hypothesis : a comparative study of vocal communication in macaques

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TESTER L'HYPOTHESE DE COMPLEXITE SOCIALE : UNE ETUDE COMPARATIVE DE LA COMMUNICATION VOCALE CHEZ LES MACAQUES

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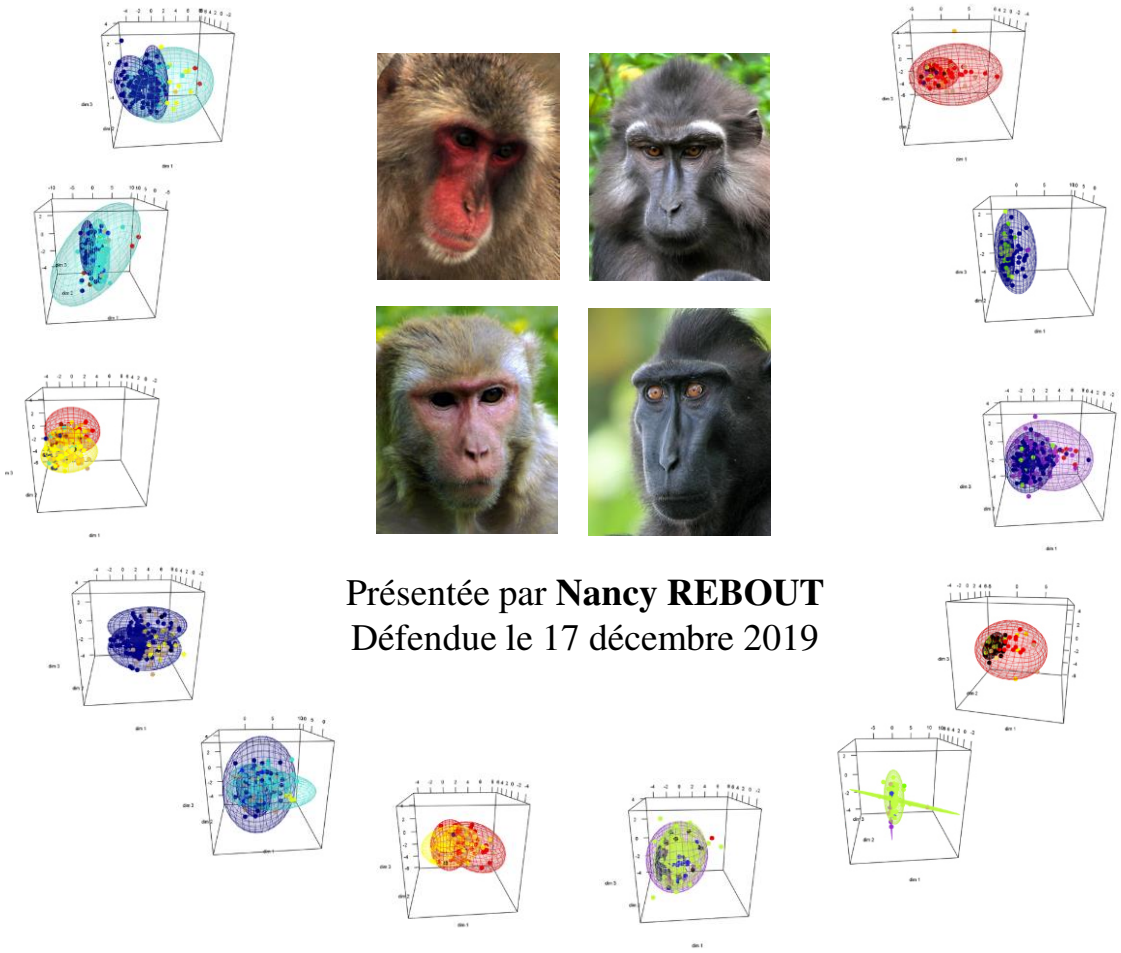

Présentée par **Nancy REBOUT**
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Résumé en Français du manuscrit de thèse :

Tester l'hypothèse de complexité sociale : une étude comparative des communications vocales chez les macaques

Doctorante

REBOUT Nancy

Mon travail de thèse a eu pour objectif de tester l'hypothèse de la relation entre complexité sociale et complexité des communications chez les macaques. Le mémoire de thèse comporte huit chapitres incluant une introduction générale, une présentation des sujets d'étude et méthodes d'enregistrement, deux chapitres théoriques, trois chapitres de résultats, ainsi qu'une discussion générale.

Chapitre 1 : Introduction générale

Mon travail de thèse vise à tester l'hypothèse de la complexité sociale dans les communications. Cette hypothèse est récemment devenue un enjeu majeur dans l'étude de l'évolution de l'organisation sociale (Freeberg et al., 2012). Elle affirme que l'organisation sociale et les systèmes de communication ont co-évolué, c'est-à-dire que des environnements sociaux complexes, qui supposent l'échange de messages d'information élaborés avec une grande diversité de partenaires, demandent aux individus d'utiliser une communication complexe.

L'introduction générale commence par une synthèse des différents types d'organisation sociale des primates, avec les définitions et mesures de la complexité sociale. Elle poursuit par les systèmes de communication et les définitions et mesures de complexité des communications et notamment la complexité vocale. Elle pose ensuite la question de l'évolution de la complexité et des indices qui ont été proposés jusqu'ici pour la mesurer. On trouve dans la littérature des études qui tentent d'établir une association entre diversité sociale et diversité vocale. Cependant, pour tester l'hypothèse de la complexité sociale, il est nécessaire d'utiliser des indices quantitatifs basés sur un cadre théorique, et cela chez un modèle animal adéquat. Les espèces de macaque sont connues pour différer dans leur degré de tolérance sociale, en relation avec le niveau d'incertitude de leurs interactions sociales, ce qui est vrai en particulier pour les interactions agonistiques (Thierry, 2007). Alors que chez les espèces intolérantes les conflits ont des conséquences claires en termes de gagnant ou perdant, chez les macaques plus tolérants les résultats restent indécis, ce qui correspond à un degré d'incertitude sociale élevé. Les espèces tolérantes sont donc considérées comme plus complexes sur le plan social, d'après la théorie de l'information de Shannon (Shannon, 1948) qui procure un cadre théorique solide pour l'étude de la complexité.

J'ai testé le lien entre complexité sociale et complexité des communications vocales chez les macaques en comparant la structure de leurs vocalisations. Plus précisément, j'ai comparé les vocalisations chez des femelles appartenant à quatre espèces de macaque caractérisées par des styles sociaux différents : macaques rhésus (*Macaca mulatta*) et macaques japonais (*M. fuscata*) qui présentent une forte intolérance sociale, liée à un fort gradient de dominance et une préférence marquée pour les individus apparentés, et macaques de Tonkean (*M. tonkeana*) et macaques à crête (*M. nigra*) qui montrent un niveau de tolérance sociale plus élevé, associé à une asymétrie de pouvoir plus modérée et un plus faible degré de népotisme.

Chapitre 2 : Méthodes générales

J'ai étudié des macaques japonais, des macaques rhésus, des macaques et des macaques de Tonkean maintenus en captivité, ainsi que des macaques à crête dans leur milieu naturel. J'ai étudié les femelles adultes, car elles représentent la catégorie d'âge et de sexe la plus représentée dans les groupes sociaux des macaques, et aussi les contributeurs les plus actifs en matière de communication vocale (Lemasson et al., 2013). Les femelles focales avaient au moins cinq ans.

Les données ont été recueillies pour 24 femelles dans deux groupes de macaques japonais au *Primate Research Institute* d'Inuyama (Japon), pour 16 femelles dans deux groupes de macaques rhésus au *Primate Research Center* de Rijswijk (Pays-Bas), pour 13 femelles dans quatre groupes de macaques de Tonkean au *Parco Faunistico di Piano dell'Albatino Rescue Centre* de Rieti (Italie) et au *Zoo de l'Orangerie* à Strasbourg (France), et pour 19 femelles dans deux groupes de macaques à crête vivant dans la *Tangkoko Nature Reserve* de l'île de Sulawesi (Indonésie).

L'objectif du recueil des données était d'échantillonner des vocalisations de l'ensemble du répertoire des femelles macaques, et ce, avec des informations contextuelles. Les individus ont été observés en utilisant un échantillonnage focal et instantané. De plus, j'ai enregistré les conflits unidirectionnels spontanés et les supplantations en utilisant l'échantillonnage par comportement (Altmann 1974) pour évaluer les rangs de dominance des macaques rhésus lors de chaque observation focale. Comme la majorité des conflits chez les macaques de Tonkean étaient bidirectionnels, j'ai recueilli les données sur les interactions agonistiques lors des tests de compétition (Thierry et al., 1994).

En utilisant les enregistrements collectés via des microphones unidirectionnel, j'ai mesuré, via le logiciel Raven©, les variables suivantes : la durée des cris, les quantiles en terme d'énergie sur le plan fréquentiel et sur le plan temporel, ainsi que l'entropie des cris.

En utilisant les comportements dictés au micro-cravate, j'ai distingué trois contextes d'émission des vocalisations : le contexte agonistique où l'émetteur du cri est impliqué dans une interaction agonistique ; le contexte affiliatif, où l'émetteur du cri est impliqué dans une interaction affiliative ; et le contexte neutre où l'émetteur n'est impliqué ni dans une interaction affiliative ni dans une interaction agonistique.

Chapitre 3 : Mesurer la complexité dans les organismes et les organisations

Pour tester l'hypothèse de complexité sociale, j'ai d'abord dû résoudre la difficulté concernant la définition de la « complexité ». Comprendre la complexité est un enjeu important en biologie, en sciences sociales, ainsi que dans d'autres domaines de recherche. L'un des principaux problèmes que pose le test de la complexité sociale est qu'il n'existe pas de consensus sur la définition de la complexité. Comme la beauté ou la structure, la complexité réside en partie dans l'œil du spectateur, quelque part entre l'ordre et le hasard, ce qui la rend difficile à définir dans un sens absolu. Une définition claire de la complexité est souvent manquante, plusieurs auteurs la définissant différemment et sans base théorique bien définie. Plutôt que de tenter de définir la complexité, il est plus opérationnel de l'aborder par ses conséquences en termes d'incertitude.

L'objectif de ce chapitre est de fournir aux chercheurs un outil permettant de comparer différents niveaux de complexité. J'ai développé une nouvelle mesure qui vise à quantifier la complexité des organismes vivants et des organisations sociales en fonction du niveau d'incertitude que ces systèmes peuvent produire. J'ai conceptualisé la complexité comme la somme de trois dimensions indépendantes : la *diversité* qui est basée sur le nombre d'éléments du système et le nombre de types de ces éléments ; la *flexibilité* qui influe sur les variations des éléments ; et la *combinabilité* qui fait référence à la connectivité, la modularité et l'imbrication des systèmes. Ces trois dimensions sont quantifiées à l'aide de la formule d'incertitude de Shannon et sont ensuite intégrées pour fournir un indice de complexité tripartite. Je fournis un exemple de calcul qui illustre l'utilisation de l'indice pour comparer la complexité des différents systèmes sociaux. L'indice de complexité se distingue donc par un fondement théorique établi à partir du degré d'incertitude, l'inclusion de modèles de flexibilité qui avaient jusqu'alors été largement négligés, et l'exigence que plusieurs aspects des systèmes soient pris en compte afin de comparer précisément leur degré de complexité. Ce nouvel indice devrait permettre de mettre en œuvre des programmes de recherche visant à comparer les niveaux de complexité des systèmes appartenant à différents domaines.

Chapitre 4 : Construire un référentiel commun pour comparer les clusters

Une difficulté à laquelle je me suis heurtée fut d'objectiver le répertoire vocal des macaques, qui constitue un système gradué. En effet, les catégories de vocalisations ne sont pas clairement délimitées, ce qui rend difficile la quantification de la diversité (nombre de vocalisations) et de la flexibilité vocale (variation entre ces catégories de vocalisations). En me basant sur des méthodes de cluster de type *soft clustering*, jusqu'alors peu utilisées dans le domaine de la communication animale, et en utilisant la formule d'entropie de la théorie de l'information de Shannon, j'ai pu évaluer la diversité et la flexibilité vocale d'une espèce.

Je devais cependant gérer l'aspect comparatif. J'ai donc proposé une méthode de construction et d'utilisation d'un référentiel commun pour permettre des comparaisons pertinentes entre les résultats d'analyses en cluster effectuées sur différents ensembles de données. L'utilisation d'un référentiel commun permet de résoudre deux problèmes différents. Le premier est le problème d'échelle. La construction d'un espace commun assigne les distances entre les éléments à la même échelle. L'objectif d'une analyse en cluster est précisément de regrouper des éléments sur la base de ces distances. Si les distances ne sont pas comparables, les résultats de l'analyse ne sont pas comparables non plus. Le deuxième problème est celui de l'approche comparative. Lorsque les distances ne sont pas comparables, le risque de comparer les grandes catégories d'un ensemble de données avec les sous-catégories d'un autre ensemble de données devient important. La construction d'un référentiel commun permet de standardiser différents ensembles de données, et ce, dans une optique comparative. L'utilisation de la méthode de *soft clustering* est particulièrement bien adaptée à l'étude des systèmes gradués. L'utilisation de méthodes de *model clustering* et de *fuzzy clustering* permet de quantifier et comparer la diversité vocale et la flexibilité vocale entre plusieurs espèces. Ces méthodes devraient avoir de nombreuses applications dans divers domaines qui vont bien au-delà de l'étude des communications animales.

À travers deux chapitres théoriques, j'ai pu établir une base solide pour tester l'hypothèse de la complexité sociale. Je l'ai ensuite utilisée pour comparer de manière quantitative la diversité et la flexibilité vocales chez les quatre espèces de macaques, sur le plan structurel ainsi que sur le plan contextuel.

Chapitre 5 : Comparaison de la structure acoustique des vocalisations chez les macaques tolérants et intolérants

Introduction. L'objectif est de tester l'hypothèse de complexité sociale au niveau de la structure des vocalisations. Je me suis concentrée sur deux composantes de la complexité : la diversité vocale, c'est-à-dire le nombre de catégories de cris, et la flexibilité vocale, c'est-à-dire le degré de gradation entre ces catégories de cris.

Méthodes. J'ai analysé les vocalisations en fonction des caractéristiques acoustiques suivantes : durée du cri, entropie, caractéristiques des quantiles d'énergie. J'ai examiné la diversité et la flexibilité vocale en fonction de trois contextes sociaux qui diffèrent en termes d'enjeux : agonistique, affiliatif et neutre. J'ai utilisé les méthodes de cluster développées au chapitre 4, et effectué des comparaisons en utilisant des modèles linéaires et des modèles linéaires généralisées. J'ai étudié dans ce chapitre les quatre espèces de macaques.

Résultats et Discussion. J'ai mis en évidence une diversité et une flexibilité vocale plus importantes chez les espèces tolérantes que chez les espèces intolérantes dans le contexte agonistique, contexte qui se caractérise par un plus grand niveau d'incertitude et donc une complexité plus élevée dans les interactions sociales. Ces différences sont moins marquées dans le contexte affiliatif et le contexte neutre. Ces résultats ne s'expliquent pas par les écarts phylogénétiques entre espèces. Ces résultats montrent que les espèces ayant des interactions sociales plus incertaines sont aussi celles qui présentent une plus grande diversité vocale et une plus grande flexibilité. Ceci vient appuyer l'hypothèse de complexité sociale et souligne le rôle du contexte social. Il apparaît qu'un niveau plus élevé de complexité vocale procure aux macaques tolérants une plus grande richesse de signaux de communication, ce qui les aiderait à faire face aux événements sociaux indécis, en particulier dans les situations de compétition.

Chapitre 6 : Comparaison des contextes d'émission des vocalisations chez les macaques tolérants et intolérants

Introduction. Le chapitre précédent traite de la diversité et de la flexibilité structurelle des vocalisations. C'est pour comprendre la diversité et flexibilité fonctionnelle que j'ai ensuite étudié les contextes d'émission des vocalisations. Un lien fort entre un signal vocal et un contexte donné implique un faible degré d'incertitude dans le système : lorsqu'il entend un cri spécifique du contexte, l'individu récepteur du signal n'a pas besoin d'information sur le contexte pour identifier les informations encodées dans la structure acoustique du cri ; au contraire, lorsqu'un cri est peu spécifique du contexte, l'incertitude sur le message est plus grande et l'individu récepteur nécessite des repères contextuels supplémentaires pour répondre de manière appropriée. Une plus grande liberté dans l'association entre la structure acoustique et le contexte d'émission des cris génère un niveau élevé d'incertitude et de complexité, car les deux concepts sont liés. C'est en considérant l'incertitude dans la relation entre la structure acoustique et le contexte d'émission des cris que j'ai pu tester l'hypothèse de complexité sociale.

Méthodes. J'ai étudié la structure des vocalisations encore une fois dans trois contextes sociaux (affilié, agonistique et neutre) pour comparer les espèces selon la force d'association entre la structure acoustique des vocalisations et leur contexte d'émission. J'ai comparé les quatre espèces de macaque, et par conséquent deux espèces tolérantes avec deux espèces intolérantes, en reprenant les variables acoustiques utilisées dans le chapitre précédent. Dans une première partie, j'ai développé une méthode à base de cluster (classification hiérarchique ascendante) et de calcul d'entropie pour quantifier le degré de chevauchement entre structure acoustique et contexte d'émission. Dans une seconde partie, j'ai utilisé une analyse par fonction discriminante pour comparer le degré de différenciation des cris de commentaires – c'est-à-dire des cris émis après une interaction sociale par un individu non impliqué dans cette interaction sociale – avec les cris émis dans le contexte neutre (sans interaction sociale) et à ceux émis pendant les interactions sociales.

Résultats et Discussion. Les résultats montrent que les macaques tolérants présentent un degré de chevauchement plus faible que les intolérants entre structure acoustique des cris et contexte d'émission. L'utilisation de signaux faiblement dépendant du contexte offre aux premiers une gamme d'expression plus large. L'étude des cris de commentaire émis par les individus qui assistent à l'interaction sociale entre les membres du groupe a également montré que leur structure acoustique contraste davantage avec les autres cris chez les macaques tolérants que chez les intolérants. Ceci permet aux individus qui font des commentaires de se distancier vocalement de leur contexte immédiat, et de communiquer ainsi des informations sur les interactions dans lesquelles ils ne sont pas directement impliqués.

Ces deux résultats montrent un degré de liberté et, par conséquent, un degré d'incertitude plus élevé, dans l'association entre la structure vocale et le contexte vocal chez les macaques tolérants par rapport aux macaques intolérants. Ces résultats sont en faveur de l'hypothèse de complexité sociale : les espèces dont les interactions sociales sont plus incertaines, et donc plus complexes socialement, sont également celles qui ont un degré de liberté plus élevé dans l'association entre structure acoustique et contexte d'émission, et donc plus complexes vocalement. Par rapport aux macaques intolérants, les macaques tolérants sont plus flexibles dans leur production vocale et ont le potentiel d'exprimer une plus grande variété de significations, ce qui leur permet de faire face à la plus grande incertitude de leur système social.

Chapitre 7 : Similitude vocale chez les macaques tolérants et intolérants

Introduction. Dans un avant-dernier chapitre, j'ai étudié l'influence des relations sociales sur la similitude vocale. Des exemples de similitude vocale ont été décrits dans les cris de contact chez plusieurs espèces de primates non humains au niveau du groupe. Ce phénomène favoriserait l'identification des membres d'un même groupe. Cependant, il est souvent difficile de vérifier que cette similitude vocale n'est pas une simple conséquence de la proximité génétique et l'impact du style social n'a jusqu'alors jamais été testé. J'ai comparé les patterns de similitude vocale entre individus chez deux espèces de macaques : une espèce intolérante (le macaque rhésus) et une espèce tolérante (le macaque de Tonkean).

Méthodes. J'ai comparé l'influence de l'appartenance à un groupe, des liens affiliatifs et de parenté, ainsi que des relations de dominance sur la similitude vocale. J'ai établi la parenté en nous basant sur le coefficient de parenté maternelle réalisée avec les données de pedigree pour chaque paire de femelles. J'ai également établi les rangs de dominance des individus de chaque groupe en me basant sur les supplantations et les conflits unidirectionnels, soit lors des enregistrements focaux chez les macaques rhésus, soit lors de tests de compétition chez le macaque de Tonkean. J'ai ensuite utilisé le logiciel SOCPROG pour déduire les rangs de dominance. J'ai évalué la similitude vocale sur la base d'une comparaison quantitative de pixels sur la forme de la fréquence fondamentale en utilisant le logiciel ANA©. J'ai comparé les résultats en utilisant des modèles linéaires mixtes (LMM).

Résultats et Discussion. Une parenté étroite a favorisé la similitude vocale entre femelles chez les deux espèces. Les relations de parenté sont à la base de l'organisation sociale des macaques et, même si le degré de népotisme varie d'une espèce à l'autre, toutes leurs sociétés sont organisées en lignées maternelles. L'appartenance au groupe a favorisé la similitude vocale chez le macaque de Tonkean et non chez les macaques rhésus. Des relations sociales plus ouvertes semblent favoriser une similitude acoustique à l'échelle du groupe chez l'espèce tolérante, alors que le phénomène de similitude vocale se produit davantage entre individus appartenant à un même sous-groupe chez l'espèce plus intolérante. Ces résultats soulignent l'implication de facteurs d'apprentissage et/ou génétique sur la similitude vocale. Chez les macaques rhésus, on observe plus de similitude entre partenaires ayant une asymétrie de dominance forte (dominantes vs. dominées) ou faibles (entre dominantes, entre intermédiaires

ou entre dominées) qu'entre celles ayant une asymétrie de dominance moyenne (dominantes vs. intermédiaires, dominées vs. intermédiaires). Ce résultat souligne encore une fois le rôle de l'expérience. Aucun effet significatif de la dominance n'a été mis en évidence chez le macaque de Tonkean. Ces résultats fournissent une preuve supplémentaire de la flexibilité des signaux vocaux produits par les macaques, et révèlent qu'elle est influencée par le style de relation sociale caractéristique de l'espèce.

Chapitre 8 : Discussion générale

Dans cette thèse, j'ai développé plusieurs outils pour mesurer et comparer la complexité des systèmes. J'ai pris en compte la nature multidimensionnelle de la complexité en définissant trois composantes : la diversité, la flexibilité et la combinabilité. Ceci m'a permis de développer des approches complémentaires et ceux à différents niveaux. J'ai alors établi une procédure permettant de comparer les signaux gradés en termes de diversité de flexibilité. J'ai également mis au point une méthode afin de comparer la force de l'association entre la structure acoustique des vocalisations et leur contexte d'émission. Ce sont ces outils quantitatifs que j'ai utilisés pour comparer les quatre espèces de macaque.

J'ai testé l'hypothèse de la complexité sociale sur deux dimensions, la diversité et la flexibilité. Cela a montré que les macaques tolérants affichent une complexité des communications vocales plus marquée que les macaques plus intolérants en termes de diversité structurelle, flexibilité et souplesse contextuelle. Leurs signaux vocaux apparaissent plus riches et plus souples que ceux de leurs homologues plus intolérants. Ces variations interspécifiques sont liées à la différence dans le degré d'incertitude de leurs interactions sociales. Ces résultats soutiennent l'hypothèse de l'existence d'une relation entre complexité sociale et complexité des communications. Ils apportent une lumière nouvelle sur l'évolution des systèmes de communication chez les primates, avec en particulier l'intervention de contraintes de structure internes aux systèmes sociaux.

Mes travaux de thèse se sont concentrés sur la communication vocale en étudiant la production de signaux. Une perspective logique de ma thèse est donc d'étudier maintenant la réception des signaux vocaux, par le biais d'expériences de repasse par exemple. Une autre perspective importante de ma thèse est d'étudier la troisième dimension de la complexité. En effet, l'examen de la diversité de la flexibilité était une étape nécessaire pour étudier cette dernière dimension, la dimension combinatoire : la prochaine étape est de tester l'hypothèse de la complexité sociale à travers l'analyse des séquences vocales.

PUBLICATIONS

Rebout, N., Lone, J.C., De Marco, A., Sanna, A., Cozzolino, R., Lemasson, A., Thierry B. Measuring complexity in organisms and organizations. *(soumis pour publication)*

Rebout, N., De Marco, A., Lone, J.C., Sanna, A., Cozzolino, R., Micheletta, J., Sterck, E. H., Langermans, J. A., & Lemasson, A., Thierry B (2020). Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication. *Proceedings of the Royal Society B,* 287, 20200439 (DOI : 10.1098/rspb.2020.0439)

De Marco, A., **Rebout, N.,** Massiot, E., Sanna, A., Cozzolino, R., Sterck, E. H., Langermans, J. A., Thierry, B., & Lemasson, A. (2019). Differential patterns of vocal similarity in tolerant and intolerant macaques. *Behaviour,* 156, 1209-1233 (DOI:10.1163/1568539X-00003562)

Un autre article sera soumis dans les prochains mois :

Rebout, N., De Marco, A., van den Berg, R., Sanna, A., Cozzolino, R., Micheletta, J., Sterck, E. H., Langermans, J. A., & Lemasson, A., Thierry B. Tolerant and intolerant macaques differ in the context specificity of their vocal signals. *(en préparation)*

COMMUNICATIONS ORALES ET AFFICHÉES

Rebout N., De Marco A., Sanna A., Cozzolino R., Thierry B., Lemasson A., Agonistic vocalisations in tolerant and intolerant macaques : a test of the social complexity hypothesis. Communication orale, *9th European Conference on Behavioural Biology, Liverpool, août 2018.*

Rebout N., De Marco A., Sanna A., Cozzolino R., Thierry B., Lemasson A., Vocalisations agonistiques chez les macaques tolérants et intolerants : un test de l'hypothèse de complexité sociale. Communication orale, *48e Colloque de la Société Française pour l'Etude du Comportement Animal, Rennes, juin 2018.*

Rebout N., De Marco A., Massiot E., Sanna A., Cozzolino R., Sterck E., Langermans J., Thierry B., Lemasson A. A comparative study of acoustic variability in tonal calls of tolerant and intolerant macaques. Communication affichée. *35th International Ethological Conference, Estoril, Portugal, août 2017.*

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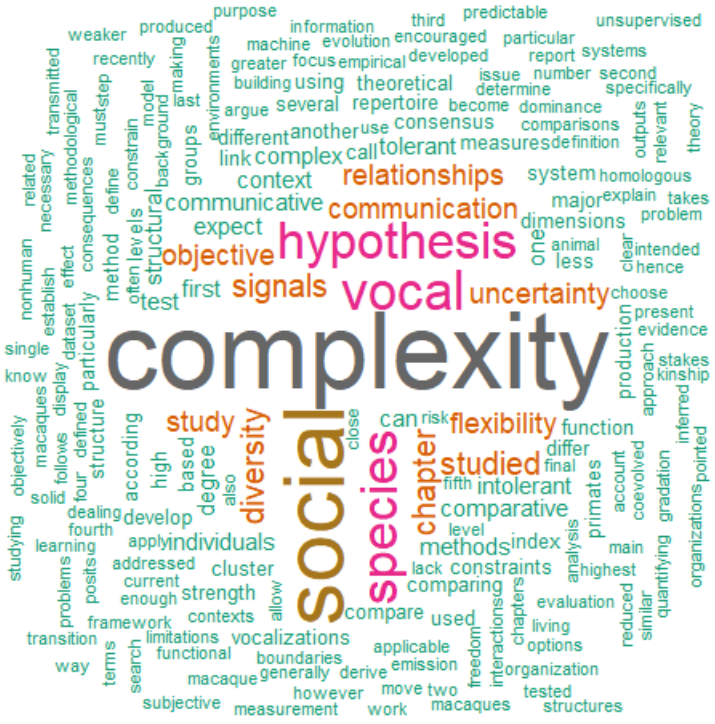
CHAPTER 1
General introduction



The evaluation of the *social complexity hypothesis for communicative complexity* has recently become a major issue in the study of the evolution of social organization. This hypothesis posits that social organizations and communication systems have co-evolved and, more specifically, that individuals living in more complex social environments should use more complex communication. The problem with complexity is that there is no consensus on its measurement, and complexity is generally defined subjectively or empirically. It is, therefore, necessary to first establish a theoretical framework to quantify complexity, then derive relevant measures of social and vocal complexity, and define a model. The social complexity hypothesis can then be tested by comparing communication signals in animal species of different levels of social complexity and communicative complexity. These species must be close enough to each other to allow homologous comparisons of related species, and display sufficiently varied and complex social relationships. Hence, I chose to focus on the study of non-human primates.

In the following, I will first report what we know about social complexity and vocal complexity in primates. I will then present the social complexity hypothesis for communicative complexity, with current evidence and limitations, and argue how complexity can be addressed using information theory. In the last step, I will explain how the comparative study of macaques can be used to test the social complexity hypothesis.

1. Social complexity

Before addressing the complexity of social systems, I will briefly review the several dimensions of social organization in non-human primates and their determinants.

1.1. Dimensions of social systems

Social systems are complex phenotypes both in structure and function. We can recognize three main dimensions in the social organization of non-human primates: demographic structure, social structure, and mating system (Kappeler and van Schaik 2002).

1.1.1. Demographic structure

The demographic structure can be characterized by group size, sex and age composition, and levels of spatial and temporal cohesion. We can recognize three main types of social

organization according to the number of animals: solitary species, pair-living species, and group-living species. Solitary species are found among prosimian nocturnal species (Radespiel 2000; Fuentes 2007). For example, the pair-living species system can be found in titi monkeys (*Callicebus cupreus*), (Norconk 2007) or gibbons (*Hylobates sp.)* (Palombit 1996); these species are often territorial, and the group generally consists of a heterosexual pair and their offspring. Individuals leave their native group at sexual maturity. Other species live in larger groups containing several females and their offspring, with either a single male, as in many langurs and guenons (uni-male groups), or several males, as in macaques and baboons (multi-male groups). Some species form multi-level societies. For example, geladas (*Theropithecus gelada*) live in a multi-level organisation composed of small units where each male forms bonds with several females (Gustison et al. 2012); this leads to several small units forming larger groups such as bands and troops (Kawai et al. 1983). Primate species also differ in the level of the spatiotemporal cohesion within their social systems. For example, chimpanzees (*Pan troglodytes*) live in a fission-fusion community where individuals can move alone or in subgroups; they form groups of variable composition, associating for a period of time and splitting up at other times (Stumpf 2007; Ramos-Fernandez et al. 2018).

Dispersion patterns influence the demographic structure and vary from one species to another. In macaques, males emigrate at adulthood (Thierry 2007), resulting in a group composition based on matrilines, i.e. subgroups based on maternal descent. In chimpanzees, on the contrary, it is the females that disperse (Stumpf, 2007 p329). In gorillas, both males and females disperse (Robbins, 2007 p311). Depending on their past interactions, individuals react differently to partners. The grouping patterns may consequently vary according to affinities, hostilities and so on. This shapes the spatiotemporal distribution of individuals within populations and influences the composition and cohesiveness of social groups.

1.1.2. Social structure

Hinde (1976) defined three levels in the social organization: social interactions, social relationships, and social networks. Social interactions refer to any action of one individual against another. These are the individual's behaviours such as actions or communication signals. For example, an individual threatens another. Social interactions differ between species in terms of nature, frequency, and intensity. Each interaction is associated with a certain emotional charge and valence. Social relationships involve a succession of interactions between individuals known to each other. For example, the sum of agonistic interactions between two individuals results in a dominance relationship between them. After a certain period of time, the relationship can be described as more or less strong. Previous interactions between two individuals may, therefore, influence future social interactions and affect the expectation of

reaction during new interactions. Primates have knowledge of the relationships between other members of their group. They react not only according to the relationship they have with their interaction partner but also according to the potential supports they can recover and the other individual can recover. Lastly, the social network is defined as the set of social relationships between the members of the group. For example, the network of dominance relationships is the social hierarchy.

1.1.3. Mating system

Monogamy, the mating system including one female and one male that mate exclusively during mating period (Fuentes 2007), is a rather rare system in non-human primates, and is found in New World monkeys and gibbons. Polyandry, a system where one female mates with more than one male during mating periods (Fuentes 2007), is also quite rare, it is found in some callitrichids where one adult female can suppress reproduction in other females, or if there is only one female (Fuentes, 2007). Absolute polygyny, a system in which one male mates with several females during the mating period, is also quite rare in non-human primates, except in species that are highly successful in mate guarding or in species with a high proportion of uni-male groups, including many langurs and guenons. Polygamous systems are the most frequent in non-human primates. In Old World monkeys such as baboons and macaques, several males mate with several females. In these species, females are particularly promiscuous and generally seek opportunities to mate with different males during the same conceptive cycle. In species where infanticide occurs, multiple mating by females is considered a strategy to confuse males for paternity (Hrdy 1979; van Noordwijk and van Schaik 2004).

The main differences in primate mating systems are their relative potential for variance in reproductive success (Fuentes, 2007). In polygynous or polygamous species, when competition for access to females is strong, males have a reproductive success that is variable. In the polyandrous system, there is a lot of variance in reproductive success because matings occur mainly between the highest-ranking female and some males. In the monogamous system, reproductive success is more balanced between individuals and also between sexes.

The number of females in a group as well as their degree of reproductive synchronization are key determinants of male monopolization of females (Kappeler and van Schaik 2002). Indeed, it is the spatial distribution of females and their degree of synchronization of the oestrus that determine the operational sex ratio, i.e. the ratio between the number of fertilizable females and the number of sexually active males (Cowlishaw and Dunbar 1991; Emlen and Oring 2007). The operational sex ratio determines the ability of males to monopolize females. When, on the one hand, females are grouped in space or synchronously, no male can monopolize females; males compete for access to females because individuals move from one sexual partner to

another (Soltis 2004; Manson 2010). On the other hand, when females are solitary or in oestrus at distinct times, one male may monopolize each female during the fertile period, thus limiting her access to rivals (Paul 2004; Soltis 2004). This is a contest competition that uses the strength and endurance of individuals. In this situation, high-ranking males have privileged access to fertile females.

1.2. Determinants of social systems

The evolution and organization of animal societies are determined by two main types of constraints, environmental and structural.

1.2.1. Environmental constraints

1.2.1.1. Benefits and costs of group living

As noted above, most species of non-human primates live in groups. This reduces the risk of predation (Wilson 1975; Danchin et al. 2008) thanks in particular to collective defense. Different species may gather and form polyspecific groups (Bshary and Noë 1997), and some may benefit from the alarm calls emitted by other species as in guenons (Zuberbühler 2000). A group of baboons defending themselves against a leopard can succeed where a single individual would perish. Moreover, group vigilance reduces the risk of being surprised. Finally, group living can lead to a dilution effect (Landeau and Terborgh 1986): the larger the number of individuals in a group, the lower the probability for one of them to be caught by a predator. Living in a group promotes cooperation between individuals and increases the efficiency of resource exploitation through information sharing (Wilson 1975). In Tonkean macaques (*Macaca tonkeana*), for example, an individual can learn what another one consumed by smelling at his mouth (Chauvin and Thierry 2005). Collaborative hunting increases the probability of successfully hunting bigger prey in chimpanzees (Boesch 2002). Living in groups allows the group to defend their resources against other groups in species foraging on patchy resources such as fruit trees. Lastly, group living can be an advantage for reproduction, as mating partners are nearby and breeding aids are potentially present, which is particularly important in animals such as primates that mature over a long period of time compared to other species. Youngsters often need to be protected for several years until they reach maturity.

However, living in a group also has a cost. One of the main drawbacks of group living is it can induce conflicts of interest. Group living creates competition among group members for food resources, mating partners or even the use of space, in primates as well as in other mammals in general (van Schaik and van Hooff 1983; Schradin et al. 2010). There are two different types of competition. The first is scramble competition, where interactions between

individuals are indirect. Consumption by one individual affects resource availability for the other. This is a form of competition that occurs when resource monopolization is not possible. On the contrary, in contest competition, resources can be monopolized by a single individual, which leads to social conflicts and the development of relationships of dominance and subordination. Contest competition favours individuals with strong competitive abilities. Finally, the last drawback of group living is that proximity to others increases the likelihood of transmission of parasites or diseases (Romano et al. 2016; Duboscq et al. 2016)

1.2.1.2. Socio-ecological models

Socio-ecological models consider social systems as the results of trade-offs between environmental constraints. Wrangham (1980) developed a model where females form groups to defend unevenly distributed resources. According to his model, abundance and food distribution should influence the species' social systems because it regulates the levels of competition between individuals. When food is distributed in high-quality patches that are defendable, the benefits of between-group competitions are greater than the costs of within-group competition. Females should, therefore, live in cohesive groups with kin-related members. On the contrary, when food is more uniformly distributed, making it less defendable, females should avoid competing with their kin and should disperse. This model was then modified by taking into account the risk of predation and distinguishing between contest and scramble feeding competition (van Schaik 1989), then the action of sexual selection, which led to the so-called *Synthetic socioecological model* (Sterck et al. 1997).

However, the synthetic socioecological model fails to explain the variety of social systems existing in non-human primates (Thierry 2008; Clutton-Brock and Janson 2012). It neglects several factors such as the role of males, parasites and pathogens that spread through group life, and interspecific variation in cognitive abilities (Thierry 2008). It also neglects the evolutionary past. For macaques, the model does not take into account variations observed in the social style of macaques species (Ménard, 2004; Thierry, 2007).

1.2.2. Structural constraints

Understanding how adaptation to the environmental factors shaped the social behaviour of animals has attracted much research and is, in fact, the main objective of the entire field of behavioural ecology (Danchin et al. 2008; Davies et al. 2012). In comparison, the role of structural constraints in biology has long been a controversial issue (Gould and Lewontin 1979; Maynard Smith et al. 1985). However, environmental factors alone are not enough to explain the complexity of the social system, as shown by the influence of phylogeny. This highlights the importance of internal constraints.

Although the definition of structural constraints itself has been problematic for some time, they can, in fact, be defined as processes that limit the response of phenotypic traits to the selective action of ecological factors (Antonovics and van Tienderen 1991; Schlichting and Pigliucci 1998). These constraints arise from the existence of interconnections between traits that have occurred over the history of evolution and keep them in an entrenched state (McLennan and Brooks 2002; Wimsatt and Schank 2004; Thierry 2013). They can occur at the genomic level through mechanisms such as gene pleiotropy and linkage disequilibrium that produce multiple correlations between traits, or at the phenotypic level through trade-offs and functional relationships between various physiological, psychological and behavioural traits (Thierry 2007).

Constraints contribute to the stability of organisms and social organization, and leads to some conservativeness in the evolutionary process. Di Fiore and Rendall (1994) showed that social traits are clustered according to taxonomic groups in Old World monkeys. They present a high level of uniformity in the basic patterns of their social systems although they live in a wide variety of habitats. Patterns of female social relationships, including dominance, nepotism, dispersion, and coalition formation, appear to have been particularly conservative throughout evolutionary history. Interspecific comparisons between macaques have also shown that patterns of dominance, aggressiveness, submission and reconciliation vary consistently with phylogeny (Thierry 2007), and comparisons in the *Eulemur* genus indicate that the demographic structure of social groups is correlated with phylogenetic distance, but not with ecological variables (Ossi and Kamilar 2006).

More recently, Shultz et al. (2011) have used the phylogenetic signal of the basic demographic structures of the primate order to reconstruct the pathways of evolution leading to different types of social organization. Their tests support a stepwise model composed of several transitions, mainly unilateral, where the development of sociality moves from solitary life to loose aggregations of several males and females, to stable multi-male–multi-female groups, and then to pairs or uni-male groups. These findings mean that the evolution of some aspects of primate social systems follows directional patterns, which challenges the assumptions of the socioecological model that assumes that all transitions from one state to another to another are equally possible.

1.3. Measuring social complexity

Historically, the search for measures of social complexity has been driven by the need for testing (Humphrey 1976; Whiten and Byrne 1997). According to this hypothesis, cognitive abilities have evolved in response to a complex social world because intense social competition

creates an arm rate that leads individuals to develop increasingly sophisticated tactics. A correlation has been found, for example, between the size of social groups, an indicator of social complexity, and the relative size of the neocortex, used as an indicator of intelligence (Dunbar 1995). However, this result remains contested (Powell et al. 2017), and the main challenge is to define and measure complexity.

1.3.1. Defining complexity

A recurrent problem in addressing social complexity is the definition of social complexity (Freeberg et al. 2012a; Bergman and Beehner 2015; Fischer et al. 2017a). A more general question is to define or measure complexity. The term complexity seems easy to intuit, but it is an ambiguous term (Cochet and Byrne 2014), difficult to quantify (Bergman and Beehner 2015). In biology, complexity is often considered as a hallmark of adaptation (McShea 1991), but without tangible evidence. Like beauty or structure, complexity lies in part in the eye of the beholder, somewhere between order and randomness, which makes it difficult to define in an absolute sense. Looking for the distinctive characteristics of complex systems, it has been proposed that they are featured by properties such as high dimensionality, involvement of non-linear dynamics, occurrence of feedback loops, lack of central control, or emergence of self-organization; even though these properties appear intuitively sound, here is no agreement yet about them since none of them constitute a necessary condition for complex systems to arise (Page 2011; Schuster 2016; Kappeler 2019a).

1.3.2. Qualitative criteria for social complexity

Due to a lack of theoretical background and a common conceptual framework with a common definition of social complexity (Kappeler 2019a), several definitions have been proposed to address social complexity with qualitative or quantitative estimates.

Social systems can be qualitatively compared according to certain criteria of social complexity. Some authors consider that a fission-fusion society is more complex than other societies (Aureli et al. 2008). Others consider that stable groups are more complex than less stable groups because they involve cooperative behaviours (Wilkinson 2003), or that geladas have a higher degree of social complexity than chacma baboons (*Papio ursinus*), due to their multi-level society (Gustison et al. 2012). Some authors suggest that mating systems such as multi-male groups are more complex than others, such as multi-male systems (Shultz and Dunbar 2006), others believe that the monogamous system is particularly complex because it includes long-term bonding and requires coordination between partners (Freeberg et al. 2012a; Peckre et al. 2019). There is no longer an agreement on models of dominance relationships

(Peckre et al. 2019). Some suggest that linear dominance is more socially complex than a more egalitarian hierarchy, as it would require cognitive skills such as *transitive inference* (MacLean et al. 2008). However, a non-linear hierarchy can also be considered complex because, from the animal's point of view, there is more uncertainty, which requires more social skills (Taborsky and Oliveira 2012).

1.3.3. Quantitative measurements of social complexity

As qualitative estimates are debatable, it should be more objective to compare the complexity of social systems in a quantitative way. The number of individuals in a social group has often been considered as an indicator of social complexity (Lehmann and Dunbar 2009; Freeberg et al. 2012a; Bergman and Beehner 2015), because living in a large group means having to discriminate against a greater number of individuals, and interact with a greater diversity of social partners in a greater diversity of contexts. Sometimes, individuals in a species gather because of converging interests such as bird flocks or shoal of fish (Parrish et al. 2002). In these gregarious species, interactions may be occasional or frequent depending on the density of the aggregation. However, individuals do not seem to show a specific preference for a particular partner. Can we consider that individuals in a shoal of fishes face a higher degree of social complexity than the individuals in a monogamous species of primate? In addition to group size, some authors suggest taking the number of social roles (Blumstein and Armitage 1997; Pollard and Blumstein 2012) such as breeding females of helpers, with more complex species having a higher number of social roles: “groups with more overlapping generations, and those with more age-sex classes present, were more socially complex in their demographic roles” (Pollard and Blumstein 2012). However, it has been criticized because it does not reveal variations such as how animals interact within these groups (Shultz and Dunbar 2006). The problem with these two measures is that they do not account for how individuals interact in their groups. One idea is to base measures of social complexity on the elements of social structure, and thus the interactions between individuals, their social relationships and the structure of their social network.

It has been suggested that social complexity could be based on social network properties such as size, diameter, and modularity (Butts 2001). Concerning social interactions, Freeberg and colleagues (2012a) defined as complex a social system where “individuals frequently interact in many different contexts with many different individuals and often with many of the same individual”. Bergman and Beehner (2015) recently noted that, although the definition seems quantitative because of the terms such as ‘frequently’, and ‘many’, this definition is “difficult to distill down to a single value that can be used in comparative studies”. In an attempt

to improve this definition, they considered the relationships between individuals and suggested defining social complexity as “the number of differentiated relationships”.

If members of a species treat all conspecifics in exactly the same way, the number of differentiated relationships would be zero. If they treat each individual they regularly encounter differently, the number of differentiated relationships would, therefore, be the number of individuals they regularly encounter. But this definition is not operational (Leighton 2017). Among primates, the number of differentiated relationships is very close to the size of the groups. A final attempt to measure complexity was made by Fischer and colleagues (2017a). They identified a way to quantify social complexity using four social indices and a cluster-based approach to identify four types of relationships and then calculate an index of relationship diversity at the individual level. This method reveals the diversity of social relationships and is not related to a specific property of complexity.

In short, primate social systems can be considered as complex system, and several variables have been used to quantify social complexity. The problem with these measures is that researchers may have been tempted to adjust their definition of complexity according to what they are testing, once data are available and/or analyzed. This temptation is accentuated by the lack of a solid theoretical basis for defining and measuring complexity.

2. Communication complexity

2.1. Structure and function of communication signals

2.1.1. What is communication?

There are three main types of definitions of communication. The first type considers communication as a signal or display liable to affect the behaviour of an individual. Thus, Krebs and Davies (1993) proposed the following definition "Process in which actors use specially designed signals or display to modify the behaviour of reactors”. The second type of definition requires intentionality in communication signals: Tomasello (2008) considers that communication signals “are chosen and produced by individual organisms flexibly” and that “these signals are *intentional* in the sense that the individual controls their use flexibly toward

the goal of influencing others". The third type of definition describes communication as a transfer of information from a sending individual to a receiving individual through a signal (Wiley 2012). More specifically, Smith (1977) defines communication as "the behaviour that enables the sharing of information between interacting individuals as they respond to each other". What is missing from this definition is the inclusion of sociality because communication is a social act, so Liebal and her colleagues (2012) have defined communication as "social behaviour that can transmit information from one individual to another".

In general, communication can be characterized as *honest* when the caller of a signal benefits from stable information, when the signal is beneficial to both the caller and the listener, or *dishonest* when the transmission of a signal is manipulated to some extent (Krebs and Dawkins 1984). When the interests of sending and receiving individuals diverge, callers may try to bluff or deceive their opponents, for example on their condition or likelihood to attack, thus using a deceptive signal (Cheney and Seyfarth 2018). When individuals repeatedly interact, however, as is the case in groups of non-human primates, unreliable signals would quickly be ignored or challenged (Cheney and Seyfarth 2018). Therefore, most signals are considered as honest in non-human primates.

2.1.2. Signal, information, and meaning

Communication is mainly defined as a transfer of information in the form of a signal between an caller/signaller and a listener individual via a transmission channel (Smith 1965; Wiley 2012). The signal is then the physical medium of the information. It is a vibratory phenomenon like a wave or assimilable to a wave, such as the acoustic wave in the case of sound (Bradbury and Vehrencamp 1998). There are different channels: olfactory or chemical channels, electrical channels, visual, mechanical or acoustic channels (Bradbury and Vehrencamp 1998). In the case of sound, the signal is defined by several acoustic parameters, the main ones being the frequency that describes the pitch of the sound, the amplitude that describes the intensity of the sound, and the duration that describes the time during which a sound wave propagates. Note that the different signals a species can produce constitute their communication repertoire and each species has its own.

The information is what is encoded by an caller through a signal that is transmitted via the propagation channel (Bradbury and Vehrencamp 1998). The signal is then perceived by the listener who decodes the information, which can induce a response from him/her. It is the listener's response that allows inferring the meaning of the signal. Said differently, the meaning can be identified as the responses selected by the listener from all the responses open to it (Cherry 1955; Smith 1965). It should be highlighted that the meaning in communication not

only depends on the structure of the signal (encoding the information) but also on the context in which this signal is transmitted (Smith 1965). There is ample evidence that non-human primates consider contextual information when responding to signals (Rendall et al. 1999; Arnold and Zuberbühler 2013; Wheeler and Hammerschmidt 2013; Price and Fischer 2014). The context is "anything which can be thought of as accompanying the signal" (Smith 1965). Smith (1965) differentiates between two types, the "immediate context", i.e. the environment of the sensory inputs, such as location in space or the physiology of the individual, and the "historical context", i.e. the genetic aspects or the memory of individuals. The listener must, therefore, consider these two elements into account to deduce the meaning of a communication process.

Concerning the signal, the code lies in the variations of the parameters, relative to each other, which summarises the properties of the signal (Bradbury and Vehrencamp 1998). In the case of the acoustic signal, the variations of the frequency parameters with respect to the duration and amplitude parameters can code the information in the signal. The information is therefore what is encoded in the signal. However, strict definitions of information are often difficult to find. As a first step, it may be easier to give examples of the types of information that can be encoded. Acoustic variations can code different kind of information: information about species, group, sex or identity of the caller (Green 1975a; Rendall et al. 2004; Tanaka et al. 2006; Bouchet et al. 2013a; Price et al. 2015), or information on the physiological state of the caller. The vocal signal can also encode his/her emotion or motivation (Morton 1977), information about social affinities, social status (Candiotti et al. 2012; Lemasson et al. 2016), or even referential information, such a reproduction, predation or alimentation (Slocombe and Zuberbühler 2006; Pfefferle et al. 2008; Berthet et al. 2018). The listener decodes the information in the signal and reacts accordingly.

However, information can be more or less easy to decode. In the study of vocalizations, the vocal repertoire can be either *discrete* or *graded*. A discrete system is a system with clear discrimination between call types. On the contrary, a graded system is a system where there is no clear boundaries between the different types of vocalizations, i.e. when there is a continuum in the acoustic structures (Hammerschmidt and Fischer 1998; Wadewitz et al. 2015). The coding of information in this system is more difficult to decipher compared to a discrete system where each vocalization is clearly distinct. A graded system allows signalers potentially to convey subtle and complex information in their calls (Manser, et al., 2014). Not only the structure of the signal may make it difficult to decode the information, but also its degree of context-specificity for the signal. Some sounds provoke certain reactions of the listener, arousal or emotional response and thus the acoustic structure can partially predict the context (Morton 1977; Owren & Rendall 2001; Briefer 2012; Gustison & Townsend 2015)(Fischer and Price

2017). Owren and Rendal (1997) constructed the *affect-conditioning model* by specifying that signals can make the listener react, either directly, on the basis of acoustic variations, or according to a long-term process and conditioning. However, they may be no one-to-one mapping between internal state and specific calls, as well as no one-to-one mapping between events in the environment and specific calls (Fischer and Price 2017). "One may conclude that the code in nonhuman primate communication is underdetermined, and the relationships between event and signal, or state and signal is of statistical nature" (Fischer and Price 2017). Calls less context-specific make it more difficult for the listener to decode the information.

Thus, different information can be contained in the signal. Meaning is both deduced from the signal information and the context in which the signal is transmitted (Smith 1965). I will add that some authors use the terms *signal* and *message* as synonyms. In the following, I will avoid the term 'message' which often implies that information is the same for the caller and listener. This is not necessarily the case. The signal can be understood by the listener in the same way, in a slightly different way, or even in a completely different way from the caller.

2.2. Drivers of variability in communication

Different conditions influence the communication systems of animals such as non-human primates, and in particular their vocal communications. Intrinsic factors such as size, weight, and physiology of individuals may influence vocalizations (Fitch and Hauser 1995; Ey et al. 2007). Moreover, vocal communications may vary depending on the arousal of the caller (Briefer 2012). Depending on the arousal, the calls may vary in duration (Rendall 2003), intensity (Fichtel and Hammerschmidt 2002), and frequency (Fichtel and Hammerschmidt 2002; Sugiura 2007) or be transmitted at a higher rate (Lemasson et al. 2010, 2012). Extrinsic factors may also influence vocal communications. Vocal signals can also vary according to the physical and social environment.

2.2.1. Physical environment

The structure of the habitat affects the visibility of individuals, which has an impact on communication modalities. Vocal communications are for example favoured over visual communications in dense tropical forests (Marler 1967; Waser and Brown 1986). Habitat also influences the structure of vocal signals (Marler 1967). Dense vegetation or a noisy environment tends to degrade or attenuate the vocal signal during its propagation (Marten and Marler 1977), which tends to favour more robust signals and more discrete vocal repertoires (Marler 1967). Habitat affects several aspects of vocal communication, restricting calls with a given frequency window (Waser and Brown 1986). Habitat can influence the time of the day

when the individuals vocalize most (Waser and Brown 1986). It can also influence the repetition rate as well as the modulations of the vocal signal (Waser and Brown 1986). Additionally, habitats influence the use of the calls. In particular, some species inhibit the production of calls in noisy environments (Miller et al. 2003; Roy et al. 2011). Finally, individuals can vary the acoustic structure of their vocalizations according to the distance from the group. For example, in cotton-top tamarins (*Saguinus oedipus*), individuals emit vocalizations with lower frequencies near their group mates, and at higher frequencies if the caller is more isolated (Cleveland and Snowdon 1982). Although the habitat influences several aspect of vocal production, it is rarely considered to have an influence, positive or negative, on vocal complexity (Freeberg et al. 2012a).

Predation pressure can also shape vocal communication. High predation risks promote the differentiation of alarm calls and influence the acoustic structure of alarm calls to make them more difficult for predators to detect, as assumed by the hypothesis of acoustic crypsis (Ruxton 2009). Animals should emit calls of low amplitude (Briskie et al. 1999) and higher-pitched (Marler 1955; Briskie et al. 1999) to limit detection by predators, with high frequencies being more attenuated with distance. Some species appear to modify the energy dispersion of their calls, with a greater dispersion over the frequency spectrum that limits the ability to detect predators (Redondo and De Reyna 1988; Wilson and Hare 2004). Ground squirrels emit 'whisper calls' that are ultrasonic alarm calls and therefore likely to reduce the probability of detection by predators (Wilson and Hare 2004). In some frogs (*Physalaemus pustulosus*), for example, isolated males emit few complex calls, i.e. short calls, with a low-frequency range and short sequences; males only use more complex calls when several males vocalize at the same time, i.e. when the competition for access to females is intense. Thus, the selection of complex or less complex calls is seen as a trade-off between enhanced attractiveness to females and increased predation risk. However, acoustic crypsis is a phenomenon that remains poorly studied in non-human primates.

Communication is considered to be referential when it allows individuals to transmit information about objects or events, i.e. about the external world (Marler et al. 1992). Two types of referential communication have been highlighted, functional and urgency-based. Urgency-based referential communication has been reported in ground squirrels (*Spermophilus beldingi*) and in ruffed lemurs (*Varecia variegata*) (Macedonia and Evans 1993) in the context of predation: vocalisations vary according to the speed and distance of the predator and should not refer to a specific class of predator. On the contrary, vocalizations are considered as functionally referential if they meet two criteria. The vocalizations have to be reliably produced in response to a specific stimulus, and vocalizations must be context-dependent, meaning that the vocalization alone must be sufficient to allow the listeners to respond in an appropriate way

(Evans 1997). Most research on functionally referential signals in non-human primates has focused on the context of predator encounters and food discovery. Acoustic structure, therefore, is expected to denote the predator or food type. It is known that vervet monkeys (*Chlorocebus aethiops*) give acoustically distinct calls when they encounter snakes, leopards, and eagles; playback experiments have shown for example that vervet monkeys scan the ground when they hear a snake alarm call, as they would when they discover a python (Seyfarth et al. 1980). Diana monkeys (*Cercopithecus diana*) produce two distinct alarm calls in response to eagles and leopards, and listeners respond as they would when meeting these predators (Zuberbühler et al. 1997). However, it may be asked to what extent alarm calls are referential. In vervet monkeys, calls of similar structures are given in different contexts (Price et al. 2015) although calls of different structures are given in the same context (Struhsaker 1967).

Several studies have also shown that non-human primates produce specific calls when they find food. For example, toque macaques (*Macaca sinica)* give acoustically distinct vocalizations in the presence of abundant food sources (Dittus 1984). Some species are able to modulate their calls according to food quantity and quality. Golden lion tamarins (*Leontopithecus rosalia*) produce food-associated calls at higher rates for highly preferred food (Roush and Snowdon 2000). Rhesus macaques (*Macaca mulatta*) produce five acoustically different food calls (Hauser and Marler 1993). Chimpanzees produce acoustic call variants in response to foods of different values, their calls become longer and higher pitched when the value of the food increases (Slocombe and Zuberbühler 2006), and bonobos (*Pan paniscus*) produce sequences of calls that seem to indicate food quality (Clay and Zuberbühler 2009). However, it is questionable to what extent food calls can be considered as truly referential, as such calls are sometimes associated with positive contexts other than feeding, in which case they would not be as specific as assumed for referential signals.

2.2.2. Social environment

Vocal flexibility is often defined as the individual's ability to modify an existing repertoire or add elements to it (Liebal et al. 2012), which we may call *structural flexibility*. Alternatively, vocal flexibility can be defined as the use of existing signals in different ways, or the ability to use similar signals in different contexts (Liebal et al. 2012), what we may called *functional flexibility*. Bouchet and colleagues (2013) defined vocal flexibility as a qualitative [production] or quantitative [use] modulation of a vocal signal according to the time, thus considering both structure and function.

2.2.2.1. Functional flexibility and vocal usage

Function flexibility includes the ability to use different calls in different contexts, the influence of social partners at proximity for call emission, and the flexible perception of calls by recipients. For decades, the contextual vocal flexibility of non-human primates has been considered limited, in contrast to their gestural communication. One example is the great apes, who are very flexible in using their gestural repertoire in different contexts. For example, bonobos use 50% of their gestural repertoire in several contexts (Pika et al. 2003). On the contrary, primate vocalizations have been long considered as context-specific, with a strong association between signal and stimulus (Wheeler and Fischer 2012). This is understandable for calls emitted in urgent context related to the approach of predators. Natural selection can foster the emergence of unambiguous signals that do not require integration with additional contextual information, and thus induce a rapid response in the listener. Thus, it seems normal that in some contexts, non-human primates emit vocalizations in a rather specific way; predation context with alarm calls (Cheney and Seyfarth 1980; Zuberbühler et al. 1997), copulation calls (Hauser 1996), and possibly threat calls (Owren and Rendall 1997). It is in other contexts that they can show more vocal flexibility. They appear to emit more flexible calls in relaxed situations such as play and affiliative interactions, as well as in 'more neutral' contexts (Lemasson and Hausberger 2011), as expressed by the variability in contact calls (Lemasson and Hausberger 2011; Lemasson et al. 2012) which play an important role in the socio-spatial coordination of individuals (Palombit 1992; Arlet et al. 2015; Ordóñez-Gómez et al. 2018). In red-capped mangabeys (*Cercocebus torquatus*), there is more vocal flexibility in more socially relaxed contexts (Bouchet et al. 2012). The consequence is that there may be no direct correspondence between stimulus and response, that is, calls emitted in different contexts are not necessarily different (Crockford and Boesch 2003).

The use of vocal signals in a social context may vary depending on the audience, i.e. the presence of social partners (Zuberbühler 2008; Seyfarth et al. 2010). They can modify their vocalization emission rates according to the identity of social partners, i.e. the composition of the audience. This also applies to patterns, i.e. *antiphony* when more than two animals transmit sounds among themselves in response to preceding signals, or *duet* when a male-female pair emits signals in coordination (Yoshida and Okanoya 2005). Non-human primates can adjust their vocal production within vocal exchanges. The number of responses received may depend on the social status of the caller, as shown in Campbell's monkeys (*Cercopithecus campbelli*), Japanese macaques (*Macaca fuscata*) and in common marmosets (*Callithrix jacchus*) (Chen et al. 2009; Lemasson et al. 2010, 2013a). In particular, individuals tend to respond more frequently to calls from elders (Chen et al. 2009; Lemasson et al. 2013a), and more strongly to calls from their closer social partners (Cleveland and Snowdon 1984; Biben and Symmes 1986;

Arlet et al. 2015; Levréro et al. 2019). Response latencies also seem to be socially dependent. In squirrel monkeys (*Saimiri sciureus*), they are shorter among close partners (Biben and Symmes 1986). The use of calls can therefore be flexibly adjusted, and reflects the quality of social interactions between individuals (Maciej et al. 2013).

2.2.2.2. Structural flexibility

Structural flexibility includes both modifying an existing call – leading to another sub-category of call – and combining different calls in a sequence. Individuals can modify the structure of their vocalizations to attract attention. When Japanese macaques emit long, high-pitched calls with a high degree of modulation, for example, this increases the probability of a response compared to other calls (Koda, 2004). The structure of the vocalizations emitted during vocal exchanges can also be modified to initiate an exchange. For example, male chimpanzees have been shown to modify the structure of their pant-hoots, including duration, to promote chorusing (Fedurek et al. 2013).

Non-human primates have a relatively limited number of calls in their repertoire compared to other species such as birds, and their call structure is considered to be subject to strong genetic determinism (Hammerschmidt and Fischer 2008). However, they can demonstrate a certain degree of adjustment and flexibility in their acoustic structures (Lemasson et al. 2013b; Gruber and Grandjean 2017; Lameira 2017). Thus, within a group, individuals resemble each other vocally. It can be either a phenomenon of vocal matching or a phenomenon of vocal convergence. Vocal matching occurs during vocal exchanges where individuals respond with a call acoustically similar to the previously emitted call. This phenomenon has been shown between females in Japanese macaques (Sugiura 1998), between females and their offspring in agile gibbons (*Hylobates agilis*) (Koda et al. 2013), or between males in chimpanzees (Mitani and Gros-Louis 1998). Therefore, there is no stereotypical structure specific to one or more individuals. Vocal convergence is the process by which the acoustic properties of calls emitted by different individuals match over time (Snowdon hausberger, 1997). For example, trills in pygmy marmosets (*Cebuella pygmaea*) converge between newly matched individuals (Snowdon and Elowson 1999). Vocal convergence can happen according to social relationships, with more convergence between affiliated individuals (Lemasson et al. 2011), within pairs (Levréro et al. 2019), or according to hierarchical status (Lemasson et al. 2016). The phenomenon of vocal similarity was also found at the group level for food calls, and for contact calls in chimpanzees (Crockford et al. 2004; Watson et al. 2015) and Japanese macaques (Tanaka et al. 2006), with more vocal similarity between individuals living in the same social group. On a larger scale, population variations have been described in several species including Japanese macaques (Green 1975b; Tanaka et al. 2006), Barbary macaques (*Macaca sylvanus*)

(Fischer et al. 1998) and chimpanzees (Mitani et al. 1992). The authors consider this phenomenon as a dialect, but this notion must be taken with caution because most studies have highlighted differences between groups without establishing their origin, whether acquired or under genetic control.

The vocal repertoire of each species is strongly influenced by genetics (Hammerschmidt and Fischer 2008), as shown by cross-fostering experiments (Owren et al. 1993). A parallel has been established between acoustic similarity and phylogenetic proximity in some species (Gautier 1988; Geissmann 2002). In mandrills (*Mandrillus sphinx*), the structure of contact calls is more similar between relatives than between unrelated individuals (Levréro et al. 2015). At the intraspecific level, it is often difficult to disentangle genetic and social influences. In rhesus macaques, in particular, there is more similarity between contact calls in females belonging to the same group and matriline than between females belonging to different groups and different matrilines (Pfefferle et al. 2016). These authors did not find a correlation with genetic lines and suggest instead a relation between similarity and familiarity. Other authors also argue that the similarity of contact calls is not related to genetic relatedness (Japanese macaques: Tanaka et al. 2006; Campbell's monkey: Lemasson and Hausberger 2011; bonobo: Levréro et al. 2019)

Finally, not only are non-human primates able to modify the structure of their vocal signals, but they can also combine these signals. There are three possible levels of combinatorial complexity (Ouattara et al. 2009; Lemasson et al. 2010): the general composition of the sequence, the order of the calls, and the rate of call emission. By combining calls, the number of signals and information potentially transmitted can increase and provide the basis for a more complex communication system (Arnold and Zuberbühler 2008). Several species of non-human primates can combine signals into sequences. Some striking examples of call sequences have been found in primates who produce choruses or songs. For example, males in agile gibbons produce different songs, including varying note compositions (Mitani 1988), which would fulfill a territorial function. Vocal sequences outside the context of predation or food discovery have been shown in particular in geladas (Gustison et al. 2016) and Campbell's monkeys (Ouattara et al. 2009). There is flexibility in the order of vocal units, rules when concatenating sequences. Calls can be combined in sequences by following syntactic rules that vary the meaning of vocal production. In vocal sequences), distinction is made between the lexical syntax (i.e. the arrangement of elements following certain rules, from the phonological syntax (i.e. when individuals combine two or more signals), which gives a different meaning than if each signal were produced separately (Hurford 2011; Hedwig et al. 2014).

2.3. Measures of communicative complexity

A system is often considered complex if it contains many elements and/or a large amount of information. Freeberg and colleagues (2012) have combined these two criteria in their definition of *communicative complexity*: complex communication systems "contain a large number of structurally and functionally distinct elements (e.g. large display repertoire size) or possess a high amount of bits of information".

2.3.1. Number of communication signals

For vocal communication, a greater number of different call types, i.e. vocal repertoire size, has been associated with a higher degree of vocal complexity (McComb and Semple 2005; Gustison et al. 2012; Maciej et al. 2013). To assess the size of a species' vocal repertoire, calls are generally classified by visual inspection, which is quite subjective. Quantitative approaches exist to assess the size of the repertoire, but a certain degree of subjectivity persists in the way algorithms are implemented to classify call types (Fischer et al. 2017b), which can result in highly variable repertoire sizes for the same species. There is currently no consensus on the method to be used to identify the different call types, and thus objectively determine the size of a vocal repertoire (Fischer et al. 2017b; Peckre et al. 2019). Determining the size of a vocal repertoire is even more difficult when there are variations within and between call types, i.e. when the transition from one acoustic structure to another is gradual, as in primates (Marler and Tamura 1964; Fischer et al. 2017b).

Graded vocalizations have the potential to carry rich and subtle information (Manser et al. 2014). However, a quantitative measure of the degree of gradation of repertoires is still missing, though a recent attempt is worth mentioning. Fischer (2015, 2017) have proposed using the variables of a fuzzy-clustering algorithm. This quantifies the degree of gradation between two types of calls, but it must be added that it does not yet provide a measure of the overall degree of gradation of the vocal repertoire (Peckre et al. 2019).

A repertoire with a high degree of gradation has the potential to provide more information than a repertoire with a lower degree of gradation. Combining signals in sequence is another way to increase the amount of information carried by a signal. Several authors suggest to analyze the structure and rhythmicity of vocal sequences (Kershenbaum et al. 2016). In addition, the way in which the elements of the directory are combined, particularly in the case of syntax rules, could transmit additional information and thus encode more information (Arnold and Zuberbühler 2006; Ouattara et al. 2009; Schlenker et al. 2014).

2.3.2. Information quantity

A system can be considered complex if it contains a large amount of information, which can be translated by the number of bits of information in the signals, which in turn can be estimated using Shannon entropy (Shannon 1948). It should be emphasized that Shannon's entropy is first and foremost a measure of what *could be* communicated, it represents the potential of a communication system (Shannon 1948). With regard to communication signals, some authors use Shannon entropy to quantify the diversity of vocal units in a system according to their probability of occurrence (Freeberg 2006a), i.e. the frequency of utterance for different types of calls (Bouchet et al. 2013a). Thus, a species with a repertoire of ten calls but mainly using two types of calls will be considered as a species with a lower degree of vocal complexity than a species with a repertoire of ten calls but regularly using all its call types. Other authors use Shannon's entropy or another information-theoretic measure (e.g. Markov entropy rate) to quantify the diversity of transitions in a vocal sequence (Kershenbaum 2014). A system with a larger quantity of information is a system with "a bigger tool kit of possible communicative messages, and thus also possible meaning" (Pika 2017).

2.3.3. Other proxies for vocal complexity

In addition to the two methods previously used to measure the complexity of communication systems, several authors have proposed the use of complementary variables. Some suggest to explore communicative complexity by including multidimensionality and multimodality of communication signals (Lucas et al. 2018; Peckre et al. 2019). Individuals can play on multidimensionality, for example by acting on the frequency modulation of their vocal signals: victims of attacks can exaggerate their screams according to the audience (Slocombe and Zuberbühler 2007). The use of different signaling modalities can also be considered as an indication of the complexity of communication (Liebal et al. 2012). In crested macaques (*Macaca nigra*), the use of lipsmack displays with other visual and vocal signals increases the probability of an affiliative contact in the listener (Micheletta et al. 2013). Finally, the potential of calls to encode individual information can also be considered as a marker of vocal complexity (Bouchet et al. 2013a). Some authors have even argued that referential calls or contextual and intentional usages could be considered for the study of communicative complexity (Pika 2017). To my knowledge, however, nobody has yet used them in the study of vocal complexity.

In short, the structure and function of communication systems may give way to a large amount of complexity. There is often no consensus on the definition of communicative complexity as well as social complexity. Given the graded nature of vocal repertoires and the difficulties in determining vocal categories, a simple description of the size of the repertoires is not a satisfactory indicator of vocal complexity. In some cases, a lack of clarity about terms such as vocal complexity, vocal flexibility, or vocal plasticity adds ambiguities to the definitions. Although several authors claim to have addressed complexity, they have in fact measured flexibility or diversity. For the time being, vocal complexity measurements have focused on the acoustic structure of signals and their combination rather than their use. It would be necessary to add functional complexity by studying the contexts in which calls occur.

3. The social complexity hypothesis for communicative complexity

3.1. Formulation of the hypothesis

Historically, the existence of a relationship between communication and sociality has been suggested for the first time by two pioneers of evolutionary biology, Jean-Baptiste Lamarck and Charles Darwin (Freeberg et al., 2012; Pika, 2017). Lamarck wrote "The individuals […] having largely increased their needs according as the societies which they formed became larger, had to multiply their ideas to an equivalent extent, and thus felt the need for communicating them to their fellows. We may imagine that this will have compelled them to increase and vary in the same degree the signs which they used for communicating these ideas."[1]. Therefore, the aim is to establish a link between the size of the society and the number of communication signals. Darwin (1872: p. 84) also stated that "Naturalists have remarked, I believe with truth, that social animals, from habitually using their vocal organs as a means of intercommunication, use them on other occasions much more freely than other animals".

[1] « Les individus (…) ayant considérablement multiplié leurs besoins à mesure que les sociétés qu'ils y formoient devenoient plus nombreuses, ont dû pareillement multiplier leurs idées, et par suite ressentir le besoin de les communiquer à leurs semblables. On conçoit qu'il en sera résulté pour eux la nécessité d'augmenter et de varier en même proportion les signes propres à la communication de ces idées. » (Lamarck, 1809: p. 355)

Living in a complex social system means dealing with a wide range of different social interactions and also interacting with different social partners. Social complexity should increase the need to assess and manage the behaviour of other group members. Individuals should have to discriminate between group members, express a wide range of emotional states, and transmit a wide variety of messages, which would require abilities signaling and social cognition skills (Freeberg et al. 2012a). Overall, that should increase the needs for communicative complexity.

The social complexity hypothesis for communicative complexity (Freeberg et al. 2012b; Pollard and Blumstein 2012; Peckre et al. 2019) states that communicative complexity has co-evolved with social complexity because social factors play a selective pressure in the evolution of social cognition and communication (Jolly 1966; Humphrey 1976; Dunbar 1995). Animals living in complex social systems require complex communication systems to cope with their social environment (Krams et al. 2012). It should be noted that although the social complexity hypothesis is based on the co-evolution assumption (McComb and Semple 2005), authors often assume, more or less consciously, that there is more than a correlation, and that social complexity casually leads to the evolution of communicative complexity.

3.2. Evidence for the hypothesis

Although the social complexity hypothesis applies to communicative systems in general, most of the current evidence comes from the study of vocal signals (Freeberg et al. 2012a).

3.2.1. Empirical evidence in non-primate animals

Correlations between social complexity and vocal complexity have been reported for the first time in taxa other than non-human primates. The main supports for the social complexity hypothesis were the correlations found between vocal repertoire size or information in repertoire, and the size of the group (Wilkinson 2003; McComb and Semple 2005; Freeberg 2006b; Wilkinson et al. 2019) or the number of demographic categories in age and sex (Blumstein and Armitage 1997; Pollard and Blumstein 2012).

More precisely, Ord and Garcia-Porta (2012) showed in several lizards species that dimorphism in sexual size, which is an indicator of the intensity of competition between males, was positively correlated with the number of visual ornaments considered as measures of the complexity of visual communication. Kroodsma (1977) compared the song repertoires of nine North American wrens and found more complex songs in polygynous species; he argued that strong sexual selection in polygynous mating systems has led to the evolution of complex singing behaviours. Among bats (*Saccopteryx bilineata*), the diversity of male vocal repertoire

appears to be related to the number of females on their territory (Davidson and Wilkinson 2002). In African mole-rats (*Bathyergidae*), the size of the vocal repertoire also appears to be larger in social than in solitary species (Vanden Hole et al. 2013). In whales, a correlation was found between whistles complexity (e.g. modulation and inflection points) and group size (May-Collado et al. 2007).

Based on studies in rodents, Pollard and Blumstein (2012) conclude that different aspects of sociality can guide the evolution of several aspects of communicative complexity. Social complexity (quantified in demographic terms) would explain the evolution of the size of the alarm call repertoire, while social complexity (quantified from group size) would explain the evolution of vocal individuality of alarm call (Pollard and Blumstein 2012).

3.2.2. Empirical evidence in non-human primates

Dobson (2012) showed that tolerant species of macaque have a greater repertoire of facial displays than intolerant species, and concluded that the level of social tolerance drives the evolution of signal communication in macaques. In comparing 42 species of non-human primates, McComb and Semple (2005) found a correlation between group size and vocal repertoire size. Bouchet and colleagues (2013) compared three species of non-human primates: red-capped mangabeys (living in large multi-male multi-female groups with frequent interactions between group members: the most socially complex species), De Brazza's monkeys (*Cercopithecus neglectus*) (small family groups: socially speaking the least complex species), and Campbell's monkeys (medium size harem: intermediate complexity). They found that mangabeys had higher call rates, and structurally more variable threat calls than Campbell's and De Brazza's monkeys, indicating a relationship between social and vocal complexity.

Moreover, Gustison and colleagues (2012) studied two species of primates with different social organizations: geladas, which live in a multi-level society, and chacma baboons, which live in multi-male–multi-female groups. These authors assume that geladas have a higher degree of social complexity than baboons, due to their multi-level organization. These two species share eight homologous calls, but geladas have six additional calls, considered as 'derived calls' (Gustison et al. 2012). This greater vocal diversity in geladas leads the author to claim that geladas have a higher degree of vocal complexity than baboons that would serve to maintain long-term male-female relationships (Gustison and Bergman 2016). Maciej et al. (2013) compared vocal communication of Guinea baboons (*Papio papio*), a species living in a multi-level social organization, to the vocal communication of other baboon taxa. Although they did not find a higher number of call types in Guinea baboons, they found a higher rate of affiliative calls compared to the agonistic calls of other baboon taxa, and concluded that the occurrence of more affiliative or competitive relationships drives the use of calls. According to

the authors, this is evidence that social complexity is one of the driving forces behind vocal flexibility in terms of usage.

3.3. Limitations

A first limitation of several studies conducted to test the complexity hypothesis is their circularity. If social complexity is measured by the communication signals that occur in social interactions, or if the complexity of communication is assessed in terms of social outcomes, it is not surprising to find correlations between communication and social patterns (Peckre et al. 2019). Some authors assume, without theoretical basis or empirical evidence, that a given variable is an indicator of either social or vocal complexity, and then look for correlations with several other variables that could reflect either vocal or social complexity, respectively. For example, Leighton (2017) tested the social complexity hypothesis in various bird species. In the absence of consensus on the definition of vocal complexity, he chose the size of the functional repertoire, i.e. the number of vocalizations that are used in specific behavioural contexts. To measure social complexity, he considered several aspects of sociality – including the maximal group size individuals may experience in a year, the type of cooperative breeding, and the ability to establish stable relationships – and tested their correlation with the size of the repertoire. The only correlation found showed that species that bred cooperatively had a larger vocal repertoire than non-cooperative breeding species. Leighton's results thus support the complexity hypothesis and at the same time suggests that the occurrence of cooperative breeding is an indicator of social complexity. The lack of a theoretical basis for measuring social complexity makes this conclusion spurious.

The central issue when testing the social complexity hypothesis is the absence of operational and theoretically founded measures for social complexity and communicative complexity, (Freeberg et al. 2012a; Wadewitz et al. 2015; Bergman and Beehner 2015; Fischer et al. 2017a; Kappeler 2019b, a; Peckre et al. 2019). Many studies have not been able to quantitatively measure complexity, and they only obtain evidence for a correlation between social and communication systems. In many cases, the authors tested correlations between the social or vocal components of interest to them and then they have retro-fitted their results to the complexity hypothesis (Peckre et al. 2019).

In summary, there is empirical evidence of an association between vocal and social diversity patterns in both non-human primates and other animals. However, complexity is more than diversity. To test the social complexity hypothesis of communicative complexity, we need operational measures of complexity based on a consistent theoretical framework.

4. Information theory and complexity

Despite the lack of consensus on the definition of complexity in general, it is widely recognized that the behaviour of complex systems is difficult to predict, and that the ability to produce uncertainty is their main characteristic (McDaniel and Driebe 2005; Schuster 2016). It is possible to quantify the degree of uncertainty of a system using the *entropy* value provided by the *information theory* of Shannon (1948), and to apply it to the measurement of complexity in social and communicative systems: the more evenly the elements of systems are distributed, the greater the degree of uncertainty of these systems.

4.1. Information and entropy

Information theory is a probabilistic theory developed to study the processes of encryption and information retrieval in technical systems. It was designed in an engineering context to describe the effective reproduction of a symbol across noisy physical channels (Shannon 1948). It consists of three steps: (1) the signaller encodes the information, (2) the signaller transmits the information, (3) the receiver decodes the information.

A key concept of information theory is that any objective measurement of information must be independent of its importance or meaning. Claude Shannon elaborated the idea that some signals and, more generally, events, are more likely than others. It is the probability of an event occurring that must be taken into account when measuring information. Let us take the example of a meeting between two individuals, A and B. If A always flees B when they meet, the event 'A flees B' gives no information, or at least no information that we can easily deduce. On the contrary, when A sometimes flees B but also attacks B sometimes, it is in the interest to stay and look at this interaction because we cannot predict the result *a priori*. There is uncertainty, suspense, and therefore, ultimately, information.

Let I be the information provided by the occurrence of an event, and p be the probability of such an event occurring, according to information theory we have the following relationship:

$$I = -\log(p)$$

Therefore, according to the information theory, the concepts of information and uncertainty merge and can be used in an almost interchangeable way. However, the number of events also counts. For example, during vocal communication, a species possessing 15 different calls potentially has higher quantity information than a species possessing 5 different calls. Since the

number of events, called *richness* in ecology, and their probability distribution, called *evenness* in ecology, are important in quantifying information, a metric of information needs to incorporate both. One such metric is Shannon's entropy *H*. Entropy is a fundamental concept in information theory. Let us choose here the simplest probability model considering that each signal is produced independently. Let p_i be the probability of the i^{th} type of signal and let there be *S* types of signal (or behavior). Then, the entropy is defined as:

$$H = -\sum_{i=1}^{S} p_i \log(p_i) \qquad (1)$$

When there are only two types of signal or behavior with probabilities $p_1 = p$ and $p_2 = 1 - p$, (1) becomes:

$$H = -p_1 \, log(p_1) - p_2 \log(p_2) \qquad (2)$$

Which is equivalent to:

$$H = -p \, log(p) - (1 - p) \log(1 - p) \qquad (3)$$

This is called the binary entropy function.

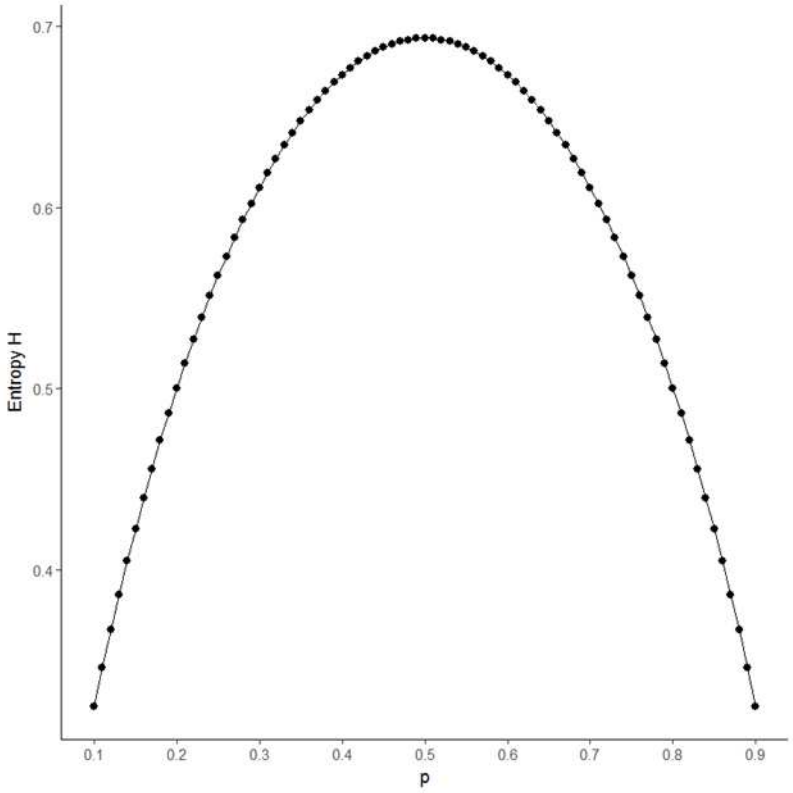


Fig. 1. Plot of the binary entropy function showing the entropy value as a function of the probability value *p*.

This binary function has a maximum value equal to log (2) (Fig. x). This maximum is reached when $p = 0.5$ and therefore $1 - p = 0.5$, i.e. when both behaviours are equally likely. When, on the other hand, the values of p are close to 0 or 1 (i.e. one of the behaviours is much more likely than the other), the resulting entropy decreases to 0; in an extreme case, only one behaviour occurs, meaning that no information is transmitted, and the entropy tends towards 0. This example can be generalized to a number of behaviours S greater than 2, which gives the same conclusion. If all probabilities are equal, so that for all i, $p_i = 1/S$, then the entropy is simply equal to the logarithm of the number of behaviours:

$$H = -S * \left(\frac{1}{S}\right) \log\left(\frac{1}{S}\right)$$

Which simplifies to:

$$H = \log(S)$$

Entropy can be used to measure the degree of uncertainty in a system. When all behaviours are equally likely, the system has a high degree of uncertainty, and entropy is at its maximum.

On the contrary, when one probability is much greater than the others, which means that one behaviour is predominant, the system has a rather low degree of uncertainty (entropy is low).

4.2. Uncertainty and complexity

The use of entropy could be problematic in a comparative approach. Two systems can have indeed the same entropy value and yet differ fundamentally. For example, a species possessing a smaller number of calls than another, but using each of its calls more equitably, may have an entropy value equal to that of a species having more calls but using certain types of calls in a biased way.

A solution is to consider independently the number of categories on the one hand and the relative proportion of these calls in the repertoire on the other hand. We must, therefore, take into account the two components of entropy, richness, and evenness. We can, therefore, compare the systems according to their number of categories, and according to the probability distributions that will be approximated by the entropy value. However, entropy depends on the number of categories. One solution is to divide entropy by its maximum, i.e. the logarithm of the number of categories, which is equivalent to calculating the relative entropy index. By using richness and evenness independently, we reconcile the two main approaches to estimating the complexity of communication systems, namely the number of signals and the amount of information. In general, considering uncertainty as an indicator of complexity can help to conclude on the complexity of a system. Previously, we had developed the example of the linearity of a social hierarchy with these two opposite points of view (see p 11) According to the uncertainty principle, a non-linear hierarchy is more complex because individuals encounter more uncertainties in their interactions.

The principle of uncertainty makes sense in the study of social and communication systems (Ramos-Fernandez et al. 2018; Cheney and Seyfarth 2018; FeldmanHall and Shenhav 2019). For example, a high degree of fission-fusion introduces uncertainty in the interactions between group members and the composition of subgroups (Ramos-Fernandez et al. 2018; Cheney and Seyfarth 2018). When two individuals come together, there is uncertainty about the outcome, as the best strategy for one depends on the response of the other (Silk et al. 2000; Cheney and Seyfarth 2018). Several authors suggest that vocalizations facilitate social interactions and reduce uncertainty about the listener's intention and behaviour (Cheney and Seyfarth 2018). In chacma baboons, for example, females tend to grunt if their partner is lower-ranked (Silk et al. 2016). They emit fewer grunts when approaching their own mothers or daughters, i.e. individuals with close and predictable bonds, than unrelated females (Silk et al. 2016). Similarly, in Japanese macaques, higher-ranking females emit a higher proportion of girneys

than lower-ranked females (Blount 1985), which would have an appeasement function in this species. Recent research has shown that when an affiliation interaction occurs between two former opponents after a conflict (Katsu et al. 2017), victims make greater use of affiliative vocalizations such as grunts, girneys, coos, toward an opponent whose behaviour is less predictable, i.e. individuals who are less familiar or higher-ranked. The use of affiliative vocalizations when approaching a lower-ranking female should reduce the uncertainty that the lower-ranking female may have about the intention of higher-ranking females.

4.3. Meaning of uncertainty and information in the sense of Shannon

In the study of animal communications, the terms 'information' and 'uncertainty' are often used in a different sense than in Shannon's information theory, leading to misunderstandings and disagreements. In the field of animal behaviour, it is common to consider information as a reduction in uncertainty (Seyfarth and Cheney 2003). From the listener's perspective, it is right that the signal conveys information that reduces its degree of uncertainty about the state of the physical or social environment, i.e. it allows the individual to better predict the outcome of current or future events (Seyfarth et al. 2010; Seyfarth and Cheney 2017). Since uncertainty is related to the concept of probability, some write that "quantity of information in a signal is measured by how far it moves probabilities" (Skyrms 2010). Fischer (2013) illustrates this with the example of alarm calls in Barbary macaques. Suppose that the presence of dogs or humans has the same probability, "After hearing a 'dog' alarm though, the likelihood that a dog is indeed present is much higher" (Fischer 2013). However, I myself consider it wrong to believe that the amount of information in the signal is measured according to 'moving' probabilities because, from a mathematical point of view, these are conditional probabilities (Albert et al., 2015 p 25). In Fischer's example, it is not the probability that the dog is present that is modified, but rather the probability that the dog is present while knowing that a dog's alarm call has been emitted. This probability is indeed higher than the probability that a dog is generally present. It should be added that even if the mathematical expression is inaccurate, an additional source of information can reduce the uncertainty of the listener in the general sense of the term, allowing the individual to better anticipate and react to her/his environment.

Uncertainty in the sense of Shannon's theory is not considered at the individual level but at the system level, and it has a specific meaning. Shannon's uncertainty is useful because it contains the notion of potential of a system, and therefore its richness. The system is unpredictable when there are a large number of options and/or these options can be resolved in different ways. Entropy allows us to assess the uncertainty of a social or communicative system, which is, in fact, the potential of this system, and thus to assess its level of complexity. It should be noted that the potential of a system can be assessed at the species level (e.g. species

repertoire) or at the individual level (e.g. individual repertoire). Shannon's information theory, however, is not suitable for studying all aspects of animal communication, as it does not address *meaning* or *semantic* (Rendall et al., 2009). Shannon & Weaver (1949) themselves emphasize it: "The word information, in this theory, is used in a special sense that must not be confused with its ordinary usage. In particular, information must not be confused with meaning. In fact, two messages, one of which is heavily loaded with meaning and the other of which is pure nonsense, can be exactly equivalent regarding information". Moving away from the meaning of the communication process can be seen as both the strength and weaknesses of information theory.

People not interested in measuring the potential of systems, as provided by information theory, can go so far as to say that the notion of information can be dispensed within the study of animal communication. Wheeler and Fischer (2012) point out that it is the listener that gives meaning to signals, so we should focus on the listener rather than using the concept of information. However, the notion of meaning is also ambiguous, at least in the way it is applied in the literature on animal communication. We currently have no explicit empirical test of significance attribution for meaning (Scarantino and Clay 2015). With regard to the present work, it should be stressed that the study of meaning would not allow the complexity of vocal systems to be addressed, or at least not in a direct way. On the contrary, this thesis focuses on the potential of systems, as it examines what different vocal structures offer in terms of expression for animals. My work aims to quantify the potential of a system, its richness, and the amount of information in order to measure the number of options available to individuals to express their emotions and intentions. By being able to link the potential of a system with its uncertainty, and ultimately its complexity, information theory and its concept of entropy appears particularly well-suited to this enterprise.

In short, the entropy value provided by information theory provides a means of measuring the uncertainty of systems, and therefore their complexity. Rather than focusing on the meaning of the signals as assigned by the listener, we can use entropy to quantify the potential of vocal systems, and thus assess the expressive range of individuals.

5. The macaque model

To test the social complexity hypothesis for communicative complexity using relevant measures of social and vocal complexity, I need to study species close enough to allow for homologous comparisons, but different enough in their social behaviours. In this respect, macaques are good candidates because they are characterized by both a profound unity in their social organization and a great diversity in their social style (Thierry 2007), with various levels of uncertainty in social relationships (Dobson 2012; Scopa and Palagi 2016).

5.1. Social system

5.1.1. Common organization

The genus *Macaca* is a monophyletic group that includes 22 species (Thierry, 2011). The fossil record indicates that they diverged from other papionini about 7 million years ago in Africa. They colonized Eurasia about 5.5 million years ago. Then, macaques branched into three phyletic lineages, the *silenus* group (e.g. *M. silenus*, *M. nemestrina*, *M. tonkeana*, *M. nigra*, *M. maurus*), the *sinica* group (e.g. *M. arctoides*, *M. radiata*, *M. thibetana*) and the *fascicularis* group (*M. fascicularis*, *M. fuscata*, *M. mulatta*), which successively colonized East Asia (Delson 1980; Delson and Rosenberger 1980; Fooden 1980; Hoelzer and Melnick 1996).

Macaques are mainly semi-terrestrial species that live in forests or semi-open habitats in South and East Asia, although one species, the Barbary macaque, still inhabits the forests of North-West Africa. Their diet consists mainly of fruits, plus leaves, buds, seeds and insects in various proportions (Ménard, 2004). They share the same basic patterns of grouping and dispersal (Thierry 2007). They live in multi-male, multi-female groups composed of adult males and females and their offspring. Neighboring groups have overlapping home ranges. Group sizes usually vary between 15 and 40 individuals. The sex ratio is biased in favour of females. Most males disperse when they reach sexual maturity and move to other groups. On the contrary, females generally remain in their native group and maintain lasting relationships with their maternal relatives. This results in a matrilineal structure with the coexistence of several generations within the same social group. Males' dominance status varies over the course of their lives according to their competitive abilities. Due to alliances between relatives, the dominance status of females is quite stable and depends on the matrilines to which they belong (Thierry, 2011).

5.1.2. Covariation between behavioural traits

Some species of macaque (e.g. Japanese and rhesus macaques) are described as *intolerant* – or 'despotic' – because they are characterized by a high intensity and asymmetry in their agonistic interactions: biting is not rare, and the recipient of aggression usually flees or submits. Conversely, other species (e.g. Tonkean and crested macaques) are described as *tolerant*, because biting is exceptional and nearly half of their social conflicts are bidirectional, where the recipient of the aggression actually protests or counter-attacks (Thierry 1985, 2000; Ciani et al. 2012; Duboscq et al. 2013). The rates of appeasement and reconciliations covary with agonistic patterns: there are lower in intolerant macaques compared with tolerant macaques (Demaria and Thierry 2001; Thierry et al. 2008). Additionally, only the latter perform peaceful interventions in conflicts, whereby a third individual approaches an opponent, often the aggressor, and stops aggression using appeasement behaviours (Petit and Thierry 1994, 2000). Other species of macaque show intermediate patterns between the first two types of species.

The correlations reported between patterns of conflict and reconciliation can be explained by proximate mechanisms (Thierry, 2000). If the risk of injury is high, the best tactic for the target of aggression is to avoid the opponent rather than to counter-attack. On the other hand, when targets can easily retaliate, initial aggressors risk becoming the recipients of dangerous attacks. While unidirectional contests and increased risk of injury inhibit the occurrence of affiliative contacts between opponents, low asymmetry and uncertainty about outcomes may create room for negotiation. By facilitating information exchange, conciliatory behaviours may thus prevent conflicts and improve social relationships.

Dominance relationships covary with agonistic patterns. In the most intolerant macaques, the gradient of dominance between individuals is steep (Flack and de Waal 2004; Balasubramaniam et al. 2017), and subordinates show clear patterns of submission: they use a facial expression, the silent bared-teeth display, to formally acknowledge their lower status relative to higher-ranking groupmates (de Waal and Luttrell 1985). In comparison, power is more evenly distributed among tolerant macaques, where the bared-teeth display has no link with dominance, but signals the peaceful intentions of the caller (Thierry et al. 1989a; Preuschoft 2004). Comparisons have shown that food competition is stronger in intolerant than in tolerant macaques, where resources are more equally distributed among group members (Petit et al. 1992; Rebout et al. 2017). The probability of lower-ranking individuals contesting higher-ranking individuals' claims over resources is higher in tolerant species, which means that the outcome of competitive interactions is more negotiable than in intolerant species (Rebout et al. 2017). When two group members compete for a resource, they must consider not only the costs of aggression and the benefits of obtaining the resource, but also the value of

their relationship (de Waal 1986). From this point of view, dominance gradient and social tolerance are in fact two aspects of the same phenomenon (Petit et al. 1992; Rebout et al. 2017).

The aforementioned differences between macaque species are associated with a long suite of behavioural variations. Females show a strong preference for their relatives in intolerant macaques, resulting in relatively close matrilines (Butovskaya 2004; Berman and Thierry 2010; Balasubramaniam et al. 2017). In contrast, kinship bias is low in tolerant macaques, meaning that females have frequent affiliative interactions with non-relatives and that matrilines remain quite open, leaving more freedom to individuals (Butovskaya 2004; Flack and de Waal 2004; Preuschoft 2004). The mother's permissiveness towards her offspring, the patterns of social play, the diversity of facial displays, and the personality dimensions of individuals show consistent variations according to levels of social tolerance in macaques (Petit et al. 2008; Ciani et al. 2012; Dobson 2012; Adams et al. 2015; Scopa and Palagi 2016).

5.1.3. Determinants of social styles

Each species of macaque can be characterized by a specific social style, i.e. a set of behavioural traits that remain relatively stable despite environmental and demographical changes. These traits are interdependent and vary in a consistent way, meaning that macaque social styles belong to a single family of forms that vary along a continuous range. Based on their patterns of aggression and reconciliation, Thierry (2000, 2007) proposed arranging macaques along a 4-grade scale going which from the most intolerant species (grade 1) to the most tolerant ones (grade 4) (Table 1).

As mentioned above, no relationship has been found so far between the social styles of macaques and the ecological conditions in which they have evolved (Ménard 2004). On the other hand, variations in social styles correlate significantly with the phylogeny of macaques (Matsumura 1999; Thierry et al. 2000b; Balasubramaniam et al. 2017). By limiting the changes possible to social organizations, interconnections between characters act as constraints that channel evolutionary processes and allow only a subset of organizations to arise. From an evolutionary point of view, social styles appear rather conservative in macaques. The good correspondence between macaque phylogeny and the 4-grade scale means that the core of the species-typical system of social relationships underwent limited changes during several hundreds of thousands of years, and even millions of years in some species.

Table 1. Scaling of macaque social styles (from Thierry 2007).

Grade 1	Grade 2	Grade 3	Grade 4
rhesus macaque *(M. mulatta)*	longtailed macaque *(M. fascicularis)*	Barbary macaque *(M. sylvanus)*	Tonkean macaque *(M. tonkeana)*
Japanese macaque *(M. fuscata)*	pigtailed macaque *(M. nemestrina)*	liontailed macaque *(M. silenus)*	crested macaque *(M. nigra)*
	Tibetan macaque *(M. thibetana)*	bonnet macaque *(M. radiata)*	moor macaque *(M. maurus)*
	Assamese macaque *(M. assamensis)*	stumptailed macaque *(M. arctoides)*	

Social tolerance increases from left (grade 1) to right (grade 4).

5.2. Vocal communication

5.2.1. Vocal repertoire

Vocal repertoires have been established for different macaque species between the 1960s and 1990s. Green (1975) defined nine main categories of vocalizations in Japanese macaques: coo, girney, whistle and warble, squawk and squeak, chirp and bark, shriek and scream, whine, gecker, and growled sound and roars. Rowell and Hinde (1962) distinguished ten categories in rhesus macaques, differentiating between 'clear calls', which contain coo, and 'noisy calls': bark, roar, growl, shrill bark, squeak, gecker, food bark, long growl, girning, and explosive cough, which were similar call categories to those found by Peters (1983) and Lindburg (1971). Lewis (1985) distinguished six vocal categories in crested macaques: pant, coo, squeal, squawk, bark, and resonant bark, which were, in turn, similar call categories to those found by Panggur (2014). Finally, Masataka and Thierry (1993) identified fifteen categories in Tonkean macaques: tonal scream, screech, pulsed scream, noisy scream, twit, pant bark, rattle, cackle, chuckle, gecker, coo, affiliation call, warning call, œstrous call, and grunt.

The problem is that the above categories were established by ear and/or visually with spectrograms, in a more or less subjective way. This results in qualitative descriptions of vocal categories. Authors comment on the following variables: harmonic structure (rich or not), energy (mainly contained in the harmonics), fundamental frequency (continuous), abrupt pitch

change (occurrence or absence), or shape of the frequency modulation. Authors add whether a call is rather loud, harsh, or noisy. They also attempt to distinguish between tonal and atonal calls, but sometimes they can only specify that a call is predominantly tonal. For some calls, the description is more precise and includes quantitative criteria such as duration range, frequency range, and possibly a maximum pitch value. These quantitative criteria are often used in a qualitative way, for example to indicate that two calls are similar except for one criterion.

It is difficult to assess the differences and similarities between the repertoires reported by different authors, even when they use similar names. For example, the food bark is said to be different from the bark in rhesus macaques because it is longer, or the gecker and squeak are said to be similar although the gecker has a lower frequency (Rowell and Hinde 1962). In many cases, the distinctions between calls were probably suggested to the authors by the fact that their contexts of emission were different. Indeed, the context is often used to differentiate call categories, but this leads to a problem of circular reasoning when the objective is to study the use of the same vocalization in different contexts. Another problem is that repertoires do not differentiate between calls and sequences of calls. In Tonkean macaques, for example, the units of the affiliative call can actually be described as coos (see Masataka & Thierry, 1993).

The fact that the vocal repertoires of macaques are graded contributes significantly to the difficulty of establishing clear categories of vocalizations. Their repertoire appears as a continuum of vocal variations, unlike other species (e.g. guenons) where the repertoire appears more discrete because vocal units are more easily identified (Lemasson and Hausberger 2011; Bouchet et al. 2013b). In Tonkean macaques, for example, three categories of coo are reported – low, clear, and harsh coo – but overlaps exist between the three (Masataka and Thierry 1993). It is also difficult to distinguish between a noisy scream and a tonal scream. To circumvent the gradation problem, researchers end up focusing their studies on only one type of call. Coos have often been studied in Japanese macaques because they are quite diverse, yet easily distinguishable from other vocalizations (Green 1975a). Similarly, screams have often been studied in rhesus macaques (Gouzoules et al. 1984, 1998; Fugate et al. 2008). On the contrary, some authors have grouped together several categories of calls despite the fact that their acoustic structures are not homologous (e.g. girneys, coos and grunts in Japanese macaques: Katsu et al., 2017).

5.2.2. Contributions to the study of vocal communication

Historically, the study of vocalizations in macaques has led to a better understanding of the mechanisms of sound production. Laboratory studies on rhesus macaques have shown that vocal production can be conditioned by reinforcement, thus showing a certain degree of volitional control over vocal production (Sutton et al. 1973; Hage et al. 2013, 2016). It is also

in macaques that neurophysiological approaches have made it possible to discover the areas of the brain involved in vocal production (Dressnandt and Jürgens 1992). Work on the vocal tract has indicated that the vocal tract of macaques is capable of producing an adequate range of speech-like sounds that would be liable to support spoken language (Lieberman et al. 1969; Nishimura et al. 2008; Fitch et al. 2016). The acoustic basis of vocal signatures has also recently been established for the coo calls of rhesus macaques (Fukushima et al. 2015).

Cross-fostering experiments have been carried out in macaques to investigate vocal learning processes. Owren and colleagues (1992) cross-fostered infants of rhesus and Japanese macaques onto mothers of the other species. They compared the call structure of the foster species and that of the biological parents' species. However, they focused mainly on the acoustic structure of food calls and, given the variation inherent in these calls, it was not possible to determine whether the variations observed were due to interspecific contrasts or cross-fostering. In a companion paper, they studied a greater variety of calls, which revealed that young Japanese macaques developed calls specific to rhesus macaques, mainly for coos (Owren et al. 1993). On the other hand, rhesus macaques developed intermediate vocal behaviours by producing more coos than expected, indicating that cross-fostering affected the production rates of vocalizations. Further studies have shown some degree of vocal learning, especially during vocal exchanges. In Japanese macaques, females tend to match the frequency range pattern of their calls to those of other females (Sugiura 1998). In the same species, the ‘matching rule’ is relevant for adults but less relevant for young individuals that do not have enough experience in conversational rules (Bouchet et al. 2017). Adult females respect the interindividual turn-taking principle unlike juveniles (Lemasson et al. 2013a). Finally, the screams emitted by adult rhesus macaques appear more specifically linked to particular social contexts than those emitted by younger individuals, suggesting that the production of screams is subject to developmental change (Gouzoules et al. 1984).

As developed above (2.2.2.2.), the study of vocal communications in macaques has contributed to our knowledge of dialects (Green 1975b; Tanaka et al. 2006) and vocal similarity in primates (Lemasson et al. 2016; Pfefferle et al. 2016). The function of calls in group cohesion has also been studied in several macaque species. In Japanese macaques, coos emitted when group members are far apart, have a higher frequency modulation than coos emitted when the individuals are close to each other (Fugate et al. 2008). In the same species, studies suggest that greeting vocalizations serve as mediators of social relationships with partners, and more specifically those with whom individuals are least familiar (Katsu et al. 2016, 2017). In crested macaques, Micheletta and colleagues (2012) showed that females reacted more strongly to the alarm calls produced by partners with whom they were linked by strong social bonds, which can lead to better social coordination in a context of predation. The acoustic structure and occurrence context of agonistic screams have also been studied extensively in rhesus and

pigtailed macaques (*Macaca nemestrina*) (Gouzoules et al. 1984, 1998; Gouzoules and Gouzoules 1989, 1990a, 2000; Fugate et al. 2008). Gouzoules and colleagues (1998) identified four different types of screams in rhesus macaques and showed that scream subtypes could be classified according to social context. In pigtailed macaques, these authors found four different screams corresponding to four different contexts, which varied according to the dominance rank of the caller's opponent and the intensity of the aggression (Gouzoules and Gouzoules 1990b). The information conveyed regarding the opponent and the ongoing conflict could then be used by third parties to adapt their response (Gouzoules et al. 1984). Lastly, the occurrence of commenting calls have been reported in Barbary macaques, where individuals can vocalize while attending an interaction between group mates (Brumm et al. 2005). The authors suggest that such comments draw the attention of others to the event, and that they could also include an evaluation of the event, but no study has yet investigated whether these calls have a specific acoustic structure.

Finally, it should be noted that vocal communication has been mainly studied in the most intolerant species such as the rhesus or Japanese macaques. In comparison, the number of studies carried out in the most tolerant species of macaque remains rather limited (Muroyama and Thierry 1998; Gouzoules and Gouzoules 2000; Riley 2005; Micheletta et al. 2012, 2013).

In short, we have a lot of information on the social behaviour of macaques and their interspecific variations. The contrasts reported in levels of social tolerance are related to differences in the degree of freedom of individuals regarding their social relationships. In comparison, research on vocal communication in the genus has been limited to a limited number of species, and to certain topics such as vocal production learning. The graded nature of the vocal repertoire of macaques makes their study difficult, which may explain why attempts to compare the vocal signals at the interspecific level have remained relatively rare.

6. Objectives of the thesis

The purpose of this work is to test the social complexity hypothesis for communicative complexity by taking advantage of reported interspecific differences in the levels of uncertainty of social interactions in macaques.

The contrasts in macaque social styles can be understood in relation to social uncertainty (Thierry et al. 1989b; Thierry 1990; Butovskaya 2004; Flack and de Waal 2004; Duboscq et al. 2017). In the most intolerant species, the outcome of social interactions is determined to a large extent by the dominance and kinship relationships between individuals, which correspond to a low degree of social uncertainty. On the contrary, more tolerant species exhibit a higher degree of freedom in their social interactions, with more room for negotiation for social partners. In agonistic interactions, in particular, the outcome of social conflicts is quite predictable in species from grade 1 (e.g. Japanese & rhesus macaques), where the recipient of aggression flees or submits in nine out of ten cases among unrelated females, i.e. most often one individual wins and the other loses: it is one vs. zero. By contrast, in species from grade 4 (e.g. Tonkean and crested macaques), 68.0 and 45.4% of conflicts between unrelated females, respectively, involve a counter-aggression (Thierry et al. 2008), which means that there is often no clear winner and loser: the result is not one vs. zero, but rather a continuum between one and zero; the interaction keeps a high degree of uncertainty, i.e. a greater richness compared to the possibilities of outcomes.

By comparing the vocal signals produced by individuals in Tonkean, crested, Japanese and rhesus macaques, it is possible to test whether different levels of uncertainty (and therefore complexity) in their social interactions, can be associated to different levels of uncertainty (and thus complexity) in their vocal communications.

The thesis is composed of five studies: the first two are devoted to the development of analytic tools necessary for the comparative study of complexity, the other three apply these tools to the testing of the social complexity hypothesis for communicative complexity in macaques:

(1) The lack of consensus on the definition and measurement of complexity is a major problem. In this study, I introduce new metrics that aim to quantify the complexity of systems according to the level of uncertainty that these systems can produce. I consider three major dimensions of complexity: diversity based on the number of system elements and the number of types of these elements; flexibility which bears upon variations in the elements; and combinability which refers to the connectedness, modularity, and nestedness of systems. I explain how they can be quantified from Shannon's information theory, and how the resulting indices are applicable to a comparative approach.

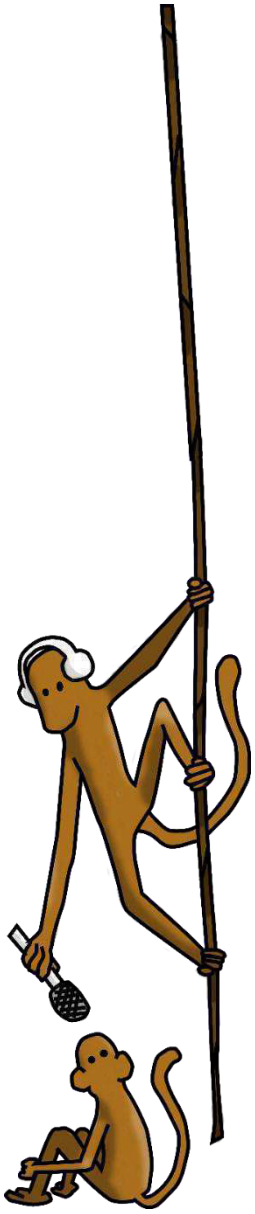
(2) In the second study, I show how to compare diversity and flexibility in several data sets. Although unsupervised machine learning methods, such as cluster analyses, are designed to find clusters within a single data set, they are not intended to compare data sets. They group the elements according to their relative distances, so that the distances in different datasets are not measured on a common scale, which prevents any direct comparison between different sets of clusters. I develop a standardization procedure based on a common frame of reference that allows the outputs of several cluster analyses to be compared.

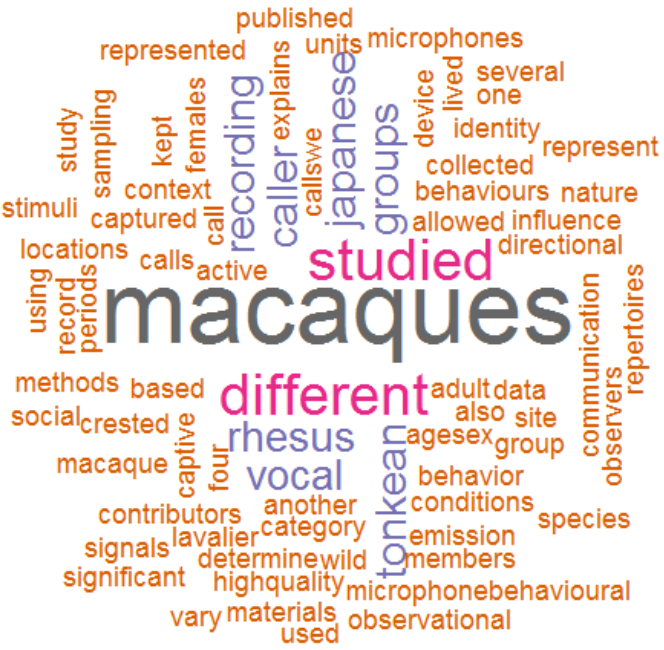
(3) The third study focuses on structural diversity and flexibility in the vocal communication of macaques. Uncertainty should be greater if the number of signals to be transmitted is higher, i.e. a higher number of call types, and if the boundaries between these signals are less clear allowing more nuances in communication. First, I measure vocal diversity by the number of call categories and vocal flexibility by the degree of gradation between these categories of call groups. I then test the following predictions drawn from the social complexity hypothesis: Vocal diversity and flexibility should be greater in intolerant than in tolerant macaques; Differences in diversity and flexibility should vary across social contexts, being strong in the agonistic context, and weak in neutral and affiliative contexts.

(4) The fourth study addresses contextual complexity. I examine the structure of vocal signals produced in three different social contexts (agonistic, affiliative, neutral) to study the specificity of the context of call emission and the form of commenting calls. Uncertainty should be greater when the degree of freedom between signal structure and context of emission of signals is higher. I test the following predictions drawn from the social complexity hypothesis: (1) *Overlap between structure and context*: analysis of the acoustic structure of calls according to the contexts in which callers are involved should reveal that the degree of overlap of acoustic structures with contexts is more pronounced in tolerant than in intolerant macaques; (2) *Differentiation in commenting calls*: analysis of the acoustic structure of comments made by bystanders should reveal that their degree of differentiation from other categories of calls – i.e. calls emitted by individuals involved in social interactions, or contact calls emitted in the absence of any interaction – is more pronounced in tolerant than in intolerant macaques.

(5) Lastly, I study the influence of social relationships on vocal production. On the basis of the social complexity hypothesis, I expect social relationships affect the structure of vocal signals more significantly in intolerant macaques than in tolerant ones. Analysing the inter-individual acoustic variation of coos emitted by females, I test the following predictions: Vocal similarity is higher between individuals bound by group membership, close kinship and/or tight affiliative bonds than between individuals not having such links; The effect of kinship and dominance relationships on vocal similarity is more pronounced among intolerant than among tolerant macaques.

CHAPTER 2
Subject and recording methods





This section describes the animals studied and their breeding conditions, as well as the sampling and recording methods. The procedures of analyses are reported in the following chapters.

1. Subjects

I studied four species of macaque. Japanese, rhesus and Tonkean macaques were kept in captive conditions, while crested macaques lived in the wild. I studied adult females because they represent the age-sex category most represented in the social groups of macaques, and also the most active contributors in vocal communication (Lemasson et al. 2013). The focal females were at least five years old. The age of individuals and their maternal kin relationships were known for the first three species. For crested macaques, the age of females was assessed based on their reproductive history since 2006 (beginning of the Macaca Nigra Project www.macaca-nigra.org), their body size, the shape of their nipples, and the presence of old physical injuries. Females were categorized as young, middle-aged or old.

The two groups of Japanese macaques originated from wild Japanese monkeys captured in Wakasa (Tottori prefecture) in 1974, and in Takahama (Fukui prefecture) in 1970/1971, respectively, (Takahashi et al. 2006). The study groups were studied at the *Primate Research Institute* of Inuyama (Kyoto University) in Japan: Wakasa group (Fw) and Takahama group (Ft) (Fig. 2). The groups were composed of 31 and 53 individuals: 10 and 17 adult males, 17 and 28 adult females, and 4 and 8 immatures, respectively. The Fw group was housed in a visually dense, wooded enclosure of 4,600 m². The Ft group was housed in a visually open enclosure of 960 m², enriched with several metal perches and shelters. Animals were fed twice a day with monkey chow and sweet potatoes. Water was available *ad libitum*.

Rhesus macaques originated from a stock imported from India to Rijswijk, The Netherlands, in the seventies (Neefe et al. 1975; Doxiadis et al. 2013). Two groups of rhesus macaques (Ma and Mb) have been studied at the *Biomedical Primate Research Center* of Rijswijk. They were founded in 2004. The groups were composed of 35 and 31 individuals, respectively: 3 and 1 adult males, 10 and 6 adult females, and 22 and 24 immatures. The two groups were housed in enclosures of approximately 210 m² and 3 m high. All enclosures were furnished with wooden structures, perches and ropes (Fig. 3). Animals were fed with commercial monkey diet pellets complemented with fresh fruit and vegetables. Water was available *ad libitum*.

Fig. 2. Enclosure for Japanese macaques at the Primate Research Institute of Inuyama.

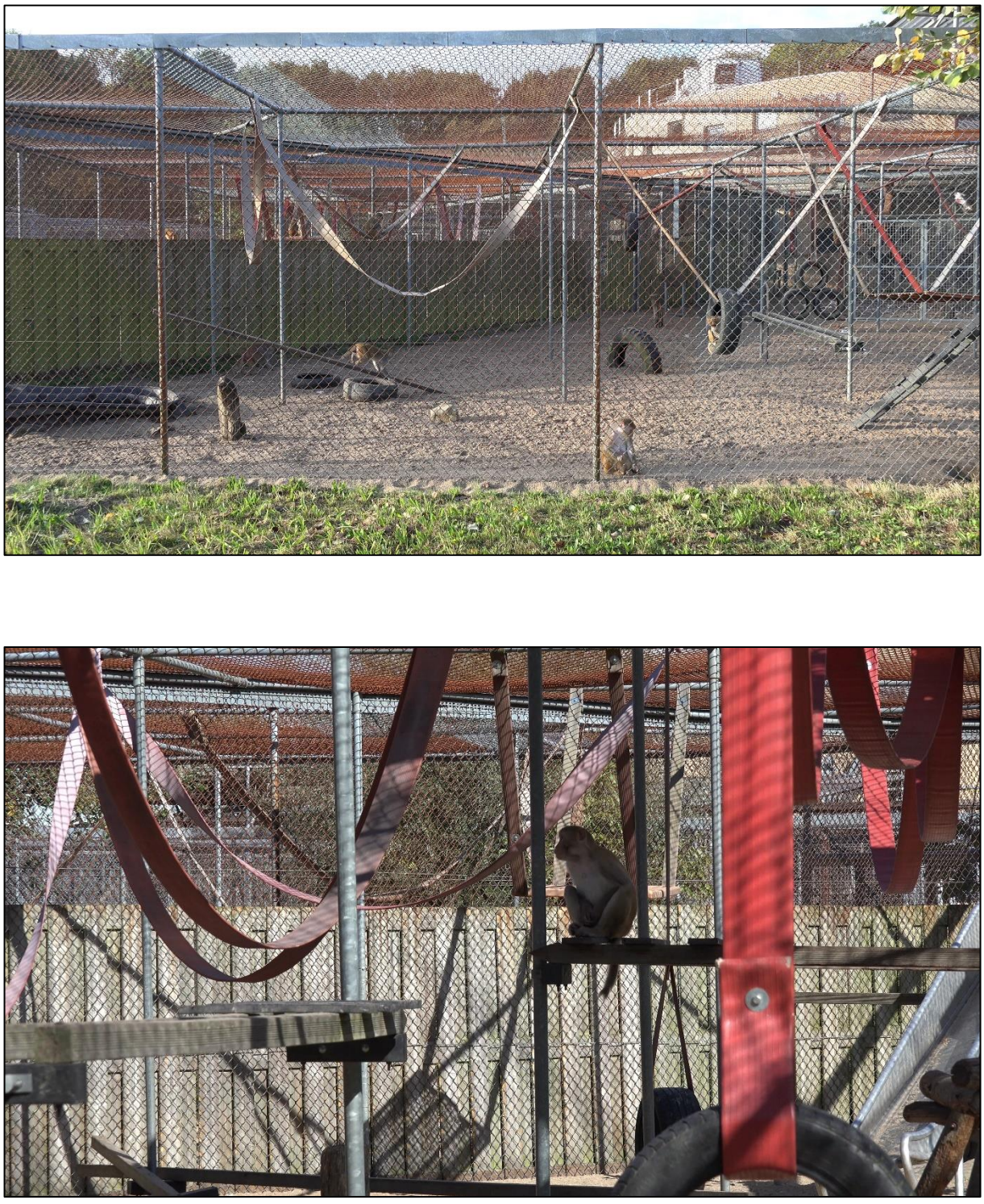


Fig. 3. Enclosures for rhesus macaques at the Biomedical Primate Research Center of Rijswijk.

Tonkean macaques originated from a stock imported into France in 1972, and has since been divided into several groups (Herrenschmidt 1977; Thierry et al. 1994). In 1978, groups Ta and Tb were split (Thierry et al. 1994). We studied group Tb and several groups (Tc, Td, Te) descending from groups Ta and Tb. Tonkean macaques from the groups Tc, Td, and Te were studied at the *Parco Faunistico di Piano dell'Abatino Rescue Centre* in Rieti, Italy (De Marco et al. 2014). I studied Tonkean macaques of the Tb groups at the *Zoo de l'Orangerie* of Strasbourg, France. Group Tb consisted of 15 individuals, 6 adult males, 4 adult females, 5 immatures. The other three groups (Tc, Td, Te), consisted of 16, 15 and 10 individuals, respectively: 4, 5 and 3 adult males, 4, 3 and 2 adult females, 8, 7 and 5 immatures. Tb group was housed in an enclosure of 120 m² and 4 m high, and Tc, Td and Te in enclosures approximately 500 m² and 5 m high (Fig. 4). Enclosures were furnished with wooden structures and perches. Commercial monkey diet pellets, fresh fruit, and vegetables were provided to the animals. Water was available *ad libitum*.

Two groups of crested macaques have been studied: Nrı and Npb. They lived in the *Tangkoko Nature Reserve* in North Sulawesi, Indonesia (Macaca Nigra Project's field site, www.macaca-nigra.org). The groups were composed of 80 and 60 individuals, respectively: 10 and 8 adult males, 28 and 23 identifiable adult females, and 42 and 29 immatures (Micheletta 2012; Duboscq et al. 2013). The habitat is broadly classified as lowland rainforest with seasonal variation in rainfall and fruit abundance; the research area was a mix of primary and secondary forests as well as old regenerating gardens (O'Brien and Kinnaird 1997) (Fig. 5). Individuals were not provisioned.

Fig. 4. Enclosures for Tonkean macaques at (a) the Parco del Albatino of Rieti, and (b) the Orangerie Zoo of Strasbourg.

Fig. 5. Crested macaques at the Tangkoko Nature Reserve, North Sulawesi.

2. Data collection

The different groups of macaques were studied in different locations and at different periods by several observers, which explains that sampling methods and recording materials could vary from one study site to another.

2.1. Sampling methods

We used focal sampling to record the behaviours of adult females (Altmann 1974). Females were sampled in a predefined random order. The vocalizations were recorded during these focal observations, in association with the behavior that followed within 3 seconds before or after the emission of a call or a sequence of calls. To ensure good recording quality, observations and recordings were conducted outdoors. We used instantaneous scan sampling (Altmann 1974) to assess social bonds between adult females by recording contact sitting and social grooming.

Data were collected in the two groups of Japanese macaques by Alban Lemasson and Ronan Jubin between February and August 2005 (Lemasson et al. 2013a, 2016; Arlet et al. 2015). Both groups were observed twice a day (morning and afternoon), for 90 mn per session, with 10-mn focal samples. This resulted in 6.1 ± 0.2 hrs of focal sampling per subject (total: 105.5 hrs). I collected data in the two groups of rhesus macaques between July and October 2016 between 09:30 and 16:30, with 15-mn focal samples. This resulted in 12.7 ± 0.7 hrs of focal sampling per subject (total: 203.25 hrs). I recorded instantaneous samples of contact sitting and social grooming every 10 mn. I collected data in one group of Tonkean macaques (Tb) from February to May 2016 between 09:30 and 16:30. Arianna De Marco and Andrea Sanna collected data in the three other groups (Tc, Td, Te) of Tonkean macaques from September 2014 to May 2015 between 11:00 and 14:00, with 15-mn focal samples in Tonkean group and 10-mn focal samples in Tonkean groups C, D and E. This resulted in 13.6 ± 3.2 hrs in Tonkean macaques (total: 177.4 hrs). They also recorded instantaneous samples of contact sitting and social grooming every 10 mn. For crested macaques, Jérôme Micheletta and an assistant carried our observations in the morning and afternoon between September 2010 and April 2011) using 30-mn focal samples. This resulted in 7.77 ± 0.4 hrs of focal sampling per individual (total: 287.5 hrs) (Micheletta 2012; Micheletta et al. 2012, 2013, 2015)

In addition to these observations using focal and instantaneous sampling, I recorded spontaneous unidirectional conflicts and supplantations using all occurrence sampling (Altmann 1974) to assess dominance ranks in rhesus macaques, during each focal observation.

As the majority of conflicts in Tonkean macaques were bidirectional, we collected additional data about agonistic interactions during competition tests (see Thierry et al. 1994). All occurrences of supplantations and unidirectional conflicts were recorded during food distribution in groups Tc, Td and Te (20 mn every morning before focal sampling). In Tonkean macaque group Tb, I recorded all occurrences of supplantations and unidirectional conflicts around a single source of orange fruit juice (seven two-hr tests) (Thierry et al. 1994).

For data collection in Japanese, rhesus and Tonkean macaques, if the focal individual was out of sight, the observer waited 2 mn. If the focal individual was out of sight for more than 2 mn, the observer turned to the next focal individual. For crested macaques, if the focal individual was out of sight, the observer waited 15 mn. If the focal individual was out of sight for more than 15 mn, the observer turned to the next focal individual.

2.2. Acoustic and behaviour records

We captured vocal signals using directional microphones and a recording device, which allowed to record high-quality calls (Fig. 6). In Tonkean and rhesus macaques, recordings were made using a Marantz© (Eindhoven, The Netherlands) PMD 661 recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. In Japanese macaques, recordings were made with a TCD-D100 Sony© (Tokyo, Japan) DAT recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and an ECM 672 Sony directional microphone. In crested macaques, recordings were made with a high-resolution camera Panasonic (Osaka, Japan) HDC-SD700 (MPG format) connected to a Sennheiser© (Wedermark, Germany) K6 and ME66 directional microphone. I extracted the sound from videos with *ffpmeg* (v 3.4.1), leading to a WAV format (sampling frequency: 32 000 Hz, resolution: 16 bits). The software Raven Pro v1.4 (Cornell Lab of Ornithology, www.birds.cornell.edu/raven) was used to draw spectrograms and measure acoustic variables (Fig. 7).

We collected observational data to determine the context of call emission: identity of the caller, behavior of the caller, behaviours of other group members, and the nature of significant stimuli that could influence the calls. In Tonkean, rhesus and Japanese macaques, we used a lavalier microphone (Tonkean and rhesus macaques: TCM 160, Meditec, Singapore; Japanese macaques: at805f, audio-technica, Leeds, United Kingdom) which was connected to the recorder to add comments about the context of the vocalizations. In crested macaques, an observer filmed the focal individual, while an assistant collected observational data using a handheld computer.

Behavioural units were based on published repertoires for macaques (Altmann 1962; Fedigan 1976; Thierry et al. 2000a) and included the following behaviours: supplantation, lunge, chase, slap, grab, bite, facial threat display, avoidance, flight, crouch, submissive facial display, approach, grasp, embrace, mount, affiliative facial display, social grooming, social play, sitting in contact, resting, monitoring, feeding.

Fig. 6. Acoustic recording in Tonkean macaques at the Orangerie Zoo.

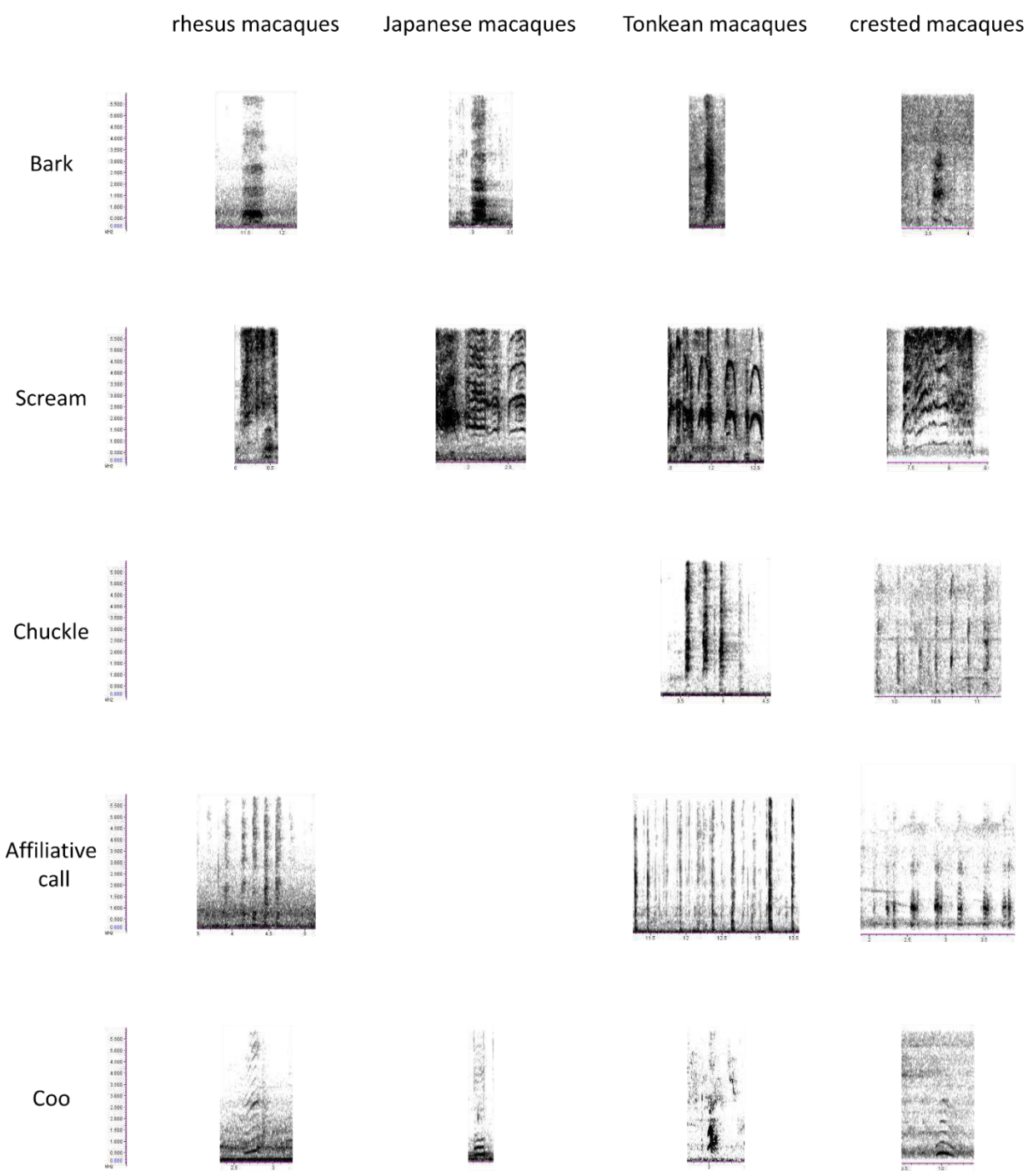


Fig. 7. Spectrogram of vocalizations for the four macaque species, drawn with the software Raven. Calls were labelled according to the categories of call types recognized in macaques (Green 1975; Lewis 1985; Lindburg 1971; Masataka & Thierry 1993; Panggur 2013; Peters 1983; Rowell & Hinde 1962).

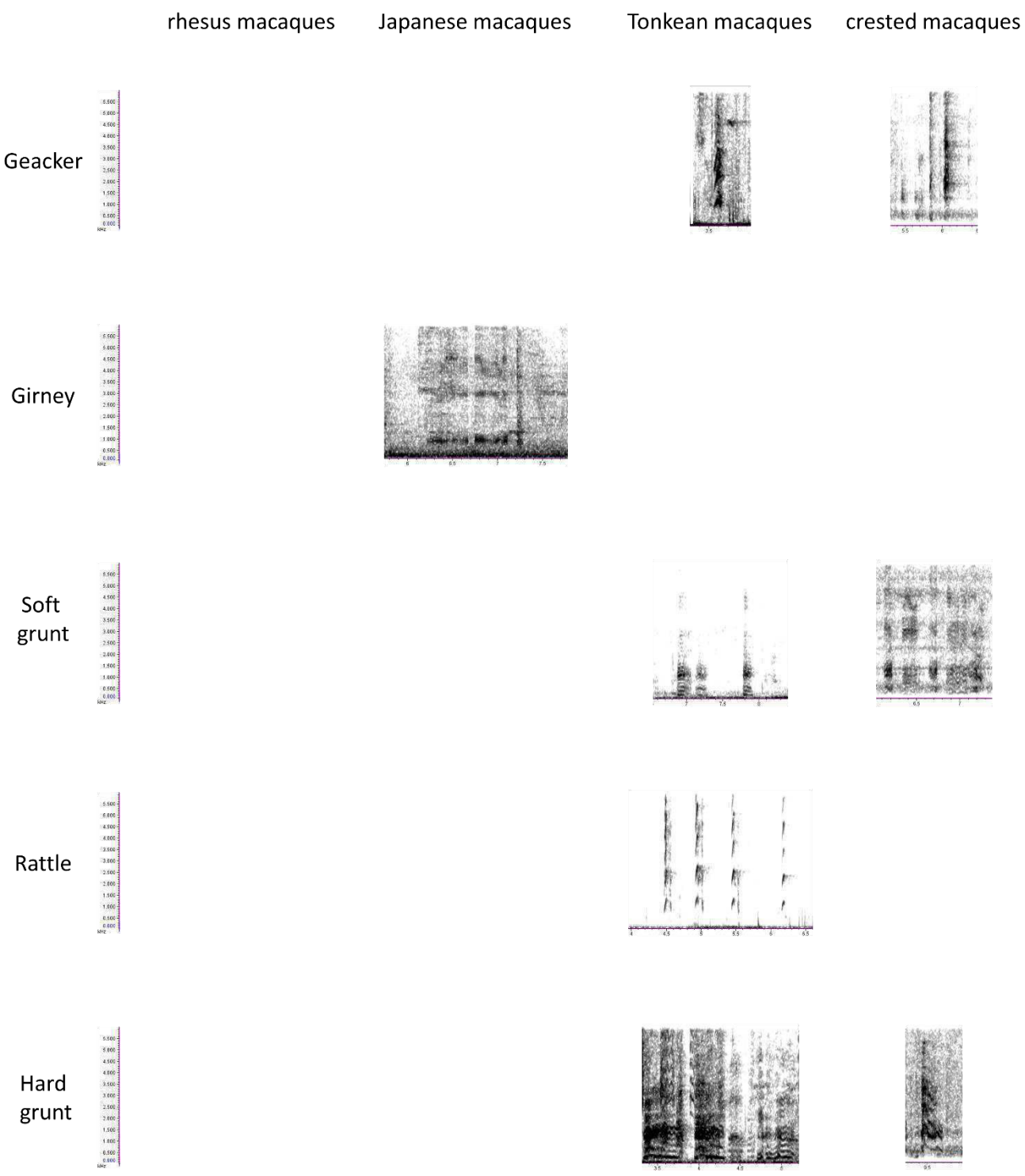
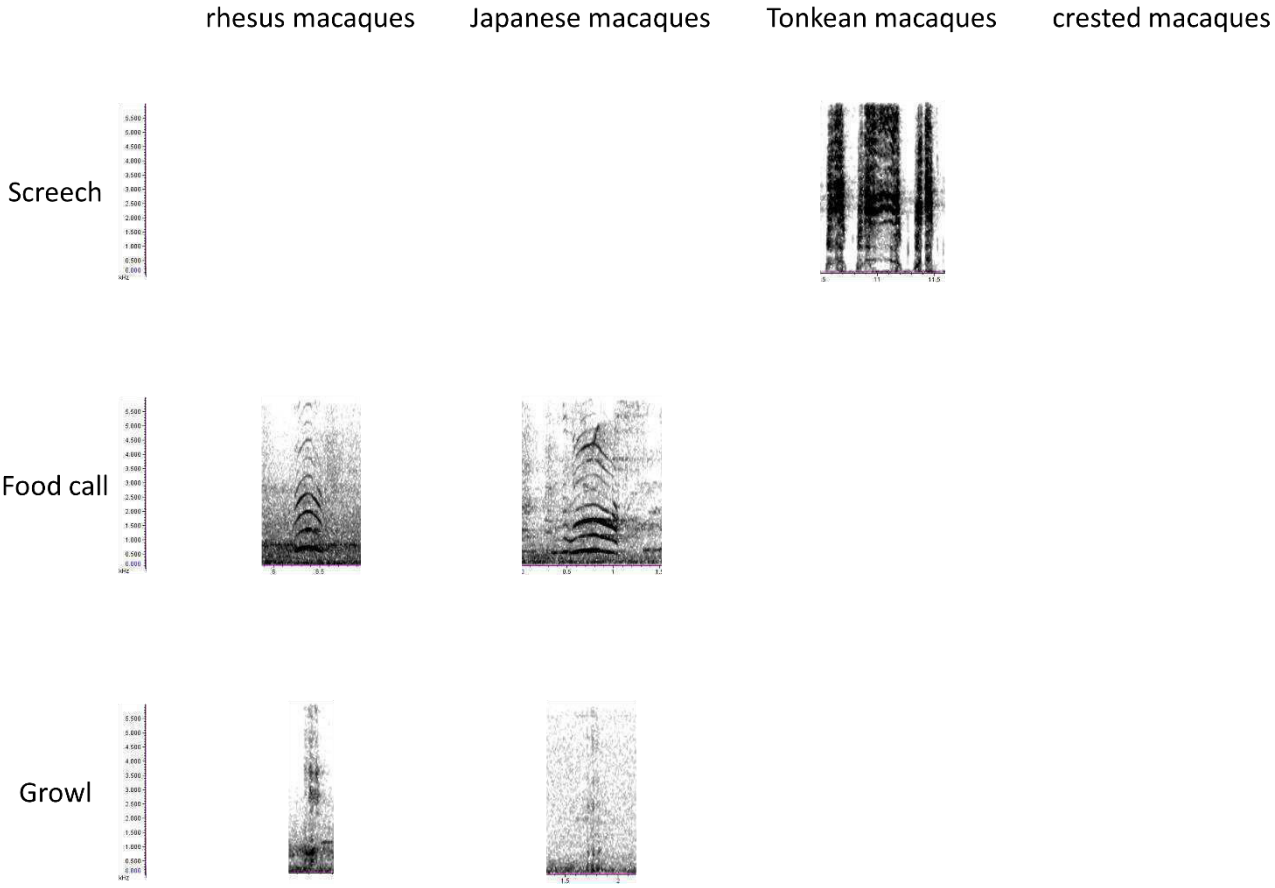


Fig. 7 continued



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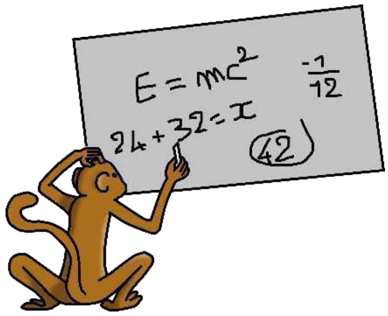
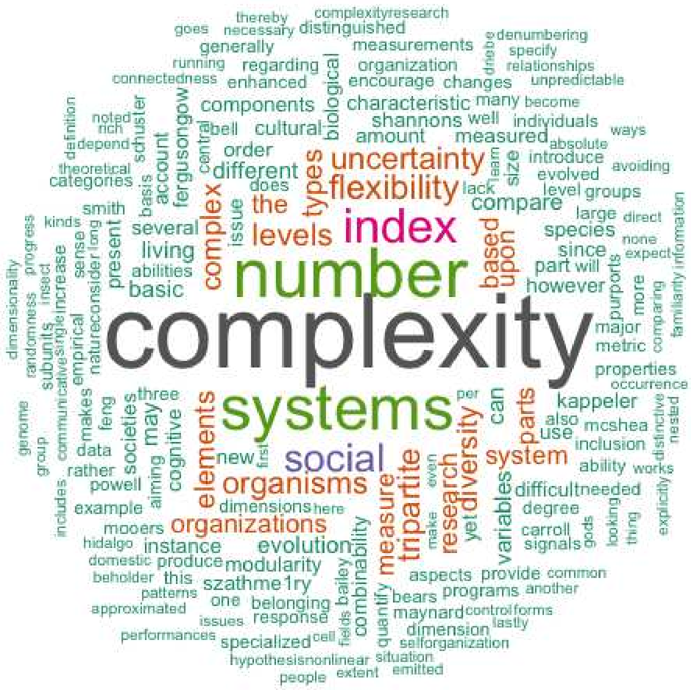


CHAPTER 3
Measuring complexity in organisms and organizations



Measuring complexity in organisms and organizations

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Abstract

We introduce new metrics that purport to quantify the complexity of living organisms and social organizations based on the level of uncertainty that these systems can produce. We consider three major dimensions regarding complexity: diversity based on the number of system elements and the number of types of these elements; flexibility which bears upon variations in the elements; and combinability which refers to the connectedness, modularity and nestedness of systems. These three dimensions are quantified using Shannon's uncertainty formula, and they can be integrated to provide a tripartite complexity index. We provide a sample calculation that illustrates the use of these indices for comparing the complexity of different social systems. Theses indices distinguish themselves by a theoretical basis grounded on the amount of uncertainty, the inclusion of flexibility patterns which had been so far largely overlooked, and the requirement that several aspects of the systems be accounted for in order to accurately compare their degree of complexity. We expect that these new complexity indices will encourage research programs aiming to compare the complexity levels of systems belonging to different realms.

Keywords

System, uncertainty, diversity, flexibility, combinability, complexity index.

Submitted manuscript

1. Introduction

Understanding complexity has become a major issue in biological and social sciences as well as in other research fields. A central question bears upon the forces that would drive biological and cultural evolution towards increasing states of complexity (Kauffman, 1993; Maynard Smith and Szathmáry, 1995; McShea, 1996, 2001; Carneiro, 2003; Carroll, 2001; Sampson et al., 2009; Muthukrishna et al., 2013; Ferguson-Gow et al., 2014; Corning and Szathmáry, 2015). A number of hypotheses have also been formulated with regard to the role of complexity in the evolution of living organisms and social organizations: Does the stability of ecological communities depend on their complexity (Feng and Bailey, 2018)? Do complex social systems need complex communicative signals (Freeberg et al., 2012)? Have enhanced cognitive abilities evolved as a response to the complexity of social life (Powell et al., 2017)? Does the complexity of human societies correlate with hierarchical organization (Turchin et al., 2017) or the spread of beliefs in moralizing gods (Whitehouse et al., 2018)? Is the gross domestic product of a country explained by its economic complexity (Hidalgo and Hausmann, 2009)? However, progress on these issues has been slow because empirical research is hindered by the lack of a well-grounded, operational measure of complexity.

Like beauty or structure, complexity lies in part in the eye of the beholder, somewhere between order and randomness, which makes it difficult to define in an absolute sense. Looking for the distinctive characteristics of complex systems, it has been proposed that they are featured by properties such as high dimensionality, involvement of non-linear dynamics, occurrence of feedback loops, lack of central control, or emergence of self-organization; even though these properties appear intuitively sound, as of yet there is no agreement about them since none of them constitute a necessary condition for complex systems to arise (Page, 2011; Ladyman et al., 2013; Schuster, 2016; Kappeler, 2019). The situation changes noticeably, however, if we consider the running of systems instead of revolving around the essence of complexity. Given that the behavior of complex systems is notoriously difficult to predict, it is widely acknowledged that the ability to produce uncertainty is their most prominent characteristic (McDaniel and Driebe, 2005; Schuster, 2016).

Here, we introduce new metrics that purport to quantify the degree of complexity of organisms and organizations based on the amount of uncertainty, irrespective of any assumption regarding the nature of complexity.

2. Complexity indices

In information theory, algorithmic complexity captures the link between complexity and uncertainty in terms of compressibility: it states that the complexity of a system is equal to the size of the minimal computational resources required to generate this system (Chaitin, 2003). As algorithmic complexity cannot be computed, Shannon's classical formula is generally used instead to measure the uncertainty regarding the outcome of a random variable associated with a given probability distribution (Shannon and Weaver, 1949). This introduces the concept of information entropy, a value quantifying the information as well as the degree of predictability of the information, which links information and complexity:

$$H = -\sum_{i=1}^{S} p_i \log p_i \qquad (1)$$

H is Shannon's entropy (or Shannon's uncertainty) index, S is the number of possible outcomes of the variable, and p_i is the probability of occurrence of each outcome i

H varies from near zero (lowest diversity when one outcome likely occurs and all other outcomes are unlikely) to a maximum value of log S (highest diversity when all outcomes are equally probable).

In a system comprised of different categories of elements, the Shannon index (H) quantifies the unpredictableness of the outcome i of a variable. Given its unifying potential, Shannon's entropy has been used in various fields and particularly in biology, where it has been applied in innumerable ways to assess the diversity of living systems. So far so good. It should be added, however, that organisms and organizations cannot be reduced to the number and distribution of their basic constituents only. Therefore, focusing the use of Shannon's entropy metric on the diversity of system elements falls short of accounting for the whole complexity of biological and cultural systems. To reconcile the measure of uncertainty with the structure and function of these systems, the calculation of diversity should be extended to further dimensions of them.

From the simple statement that a system is a set of elements that are interrelated (von Bertalanffy, 1968), it comes that systems are composed of a variable number of elements, but also that the elements themselves can be variable, and that they can associate in variable patterns. This leads us to consider three major dimensions regarding the complexity of systems: diversity, flexibility and combinability. The measurement of complexity requires that all three dimensions are accounted for, as we develop below.

2.1. Diversity index

Shannon's metric of entropy consists of two components called richness and evenness in ecology. Richness is the number of possible outcomes, types, or categories of a variable. It is a popular measure of diversity/complexity as it is relatively easy to count cell types in organisms (Valentine et al., 1994), species in ecological communities (Peet, 1974), signals in animal communication (Freeberg et al., 2012; Peckre et al., 2019), structures in languages (Nettle, 2012), or cultural variants in human societies (Carneiro, 2003). Evenness refers to the heterogeneity of probability of the different types composing the richness, whether structural or functional. In other words, eveness is the distribution law of the probabilities of the different outcomes of the variable (distribution law of p_i). It is the interplay between evenness and richness that can be used to address distribution across types.

Early on, the differentiation or specialization of system elements in discrete roles has been recognized as a clue to complexity (Limoges, 1994). Shannon's entropy is used to measure the diversity of phenomena as diverse as ecosystems, social relationships, communication signals or neural networks (e.g. Peet, 1974; Borst and Theunissen, 1999; Eagle et al., 2010; Bouchet et al., 2013; Ramos-Fernandez et al., 2018). The index was however devised to enable the comparison of indices with a different number of outcomes. It has to be adjusted to compare systems, so we will use the relative index (Pielou, 1969; Peet, 1974):

$$h = \frac{H}{H_{max}} \tag{2}$$

H_{max} is the maximal value of H, i.e. log (S)

To measure h we need to specify the different variables describing the elements of the system under consideration, and the sample space for each variable, i.e. the set of all possible outcomes. In the field of animal communication, for example, vocal signals can be described using frequencies, and we may choose a sample space based on three possible outcomes: high-pitched, medium-pitched, and low-pitched calls. Signals can also be described by their durations, leading to another sample space based on two outcomes: short-lasting and long-lasting calls.

For each variable v, we calculate a relative diversity index h_{vD} using formula (2):

$$h_{vD} = \frac{H}{H_{max}} = \frac{-\sum_{i=1}^{S_{vD}} p_i \log p_i}{\log S_{vD}} \tag{3}$$

To obtain the diversity index *D* for the system on a scale of 0 to 1, regardless of the number of variables, we calculate the mean of the relative diversity indices of the different variables:

$$D = \sum_{v=1}^{n} \frac{1}{n} h_{vD} \tag{4}$$

n is the number of variables

2.2. Flexibility index

While diversity concerns differences between types, variation can also occur within types. Contrary to systems currently envisioned by physics and engineering that are made of discrete and relatively fixed elements, living organisms and social organizations are composed of flexible elements and parts. Elements can vary, meaning that they are able to shift from one state to another, and types can intergrade, meaning that there is some probability that one element belongs to different types. Flexibility, variability or plasticity, whatever it is called, increases the unpredictability of systems, allowing them to explore functional abilities and respond to changing environments, which has a clear adaptive value (West-Eberhard, 2003; Page, 2011).

To calculate the index, we have to specify the variables describing the flexibility of elements, and the sample space for each variable. In the field of phenotypic plasticity, for example, we may choose a sample space based on the proportion of different phenotypes in a population; some butterflies show two seasonal phenotypes, dry-season and wet-season phenotypes (West-Eberhard, 2003), and therefore we can define a sample space based on both phenotypes as possible outcomes, which corresponds to possible switches from one phenotype to another.

For the variable *v*, we calculate a relative flexibility index h_{Fv} using formula (2), then a relative flexibility index similar to the relative diversity index (3):

$$h_{vF} = \frac{H}{H_{max}} = \frac{-\sum_{i=1}^{S_{vF}} p_i \log p_i}{\log S_{vF}} \tag{5}$$

The flexibility index *F* of the system is the mean of the relative flexibility indices of the different variables:

$$F = \sum_{v=1}^{n} \frac{1}{n} h_{vF} \tag{6}$$

2.3. Combinability index

System elements can interact and associate at different levels. The nature and amount of connections that occur at the dyadic level, i.e. within pairs of elements, represent a first source of uncertainty. In the study of animal behavior, for instance, it has been proposed to measure the complexity of social groups from the number and strength of relationships between individuals (Bergman and Beehner, 2015; Fischer et al., 2007; Peckre et al., 2019; Weiss et al., 2019). Connections can also arise at the triadic level, i.e. between more than two elements. In some mammals, social competition thus drives several males to associate in alliance networks, which generates subgroups of varying size and stability (Connor, 2007; Patzelt et al., 2014). More or less marked cliquishness, compartmentalization or modularity, irrespective of the designation given to it, is a general property of biological and social systems; it means that they are composed of multiple subunits that are structurally and/or functionally semi-independent (West-Eberhard, 2003). In modular organization, subunits are arranged in parallel, as for cell organelles or segmented body parts. In hierarchical organization, subunits are arranged in nested levels where larger parts are composed of smaller parts, as for organisms, organs, cells, organelles and molecules.

Counting the number of connections, modular parts or nested levels are employed to estimate complexity both in biological and social sciences (Corning and Szathmáry, 1995; McShea, 1996, 2001; Turchin et al., 2017, Bergman and Beehner, 2015). However, such methods based on separated counts remain limited. Even relatively simple systems such as bird songs can be highly combinatorial: groups of notes form syllables which are themselves assembled into phrases that are then grouped into songs, and these different subunits can appear in various combinations at multiple levels (Marler and Slabbekoorn, 2004). Instead of separately quantifying connectedness, modularity and nestedness, we may consider complex systems as sets of subunits which can vary in their degree of dissociation and differentiation, as well as in the interactions that link the units composing them.

To measure *h* we need to specify the different variables expressing the interactions between the system elements and the sample space for each variable. Consider, for example, associations of genes that have similar expression patterns across different tissue samples; such co-expressed genes are generally involved in related functions (Wen et al., 1998). We may choose a sample space based on clusters of genes as possible outcomes. The probabilities of each gene to belong to a given cluster can be used to quantify the strength of links between clusters which corresponds to a higher degree of cluster intergradation. There is more uncertainty in gene association when links between clusters are strong.

For each variable *v*, we calculate a relative combinability index h_{vC} using formula (2), then a relative combinability index similar to the relative diversity index (3):

$$h_{vC} = \frac{H}{H_{max}} = \frac{-\sum_{i=1}^{S_{vC}} p_i \log p_i}{\log S_{vC}} \quad (7)$$

The combinability index *C* of the system is the mean of the relative combinability indices of the different variables:

$$C = \sum_{v=1}^{n} \frac{1}{n} h_{vC} \quad (8)$$

2.4. Complexity index

A complexity index *K* of a given system can be drawn from its diversity, flexibility and combinability. Since the three dimension indices *D*, *F* and *C* are independently measured entropies (formulae 4, 6, 8), we calculate *K* by summing these three indices:

$$K = D + F + C \quad (9)$$

2.5. A calculation example

To illustrate the calculation of indices, we take an example from the comparative study of social systems in macaque monkeys. All macaques live in groups containing both adult males and adult females with offspring, but they display wide interspecific variation in their social relationships (Thierry, 2007). Some are characterized by strong social intolerance, meaning that they display a steep gradient of dominance coupled with conspicuous submission signals and a strong preference for kin partners. Other species show higher levels of tolerance, which correspond to moderate power asymmetries, a high propensity to regulate conflicts through affiliative behaviors, and a relatively low degree of preference for kin. It appears that strong social tolerance provides individuals with large degrees of freedom in social interactions and relations, whereas weak tolerance lends more weight to the influence of social status on individual behaviors, with presumably more predictable outcomes (see Thierry, 2007; Duboscq et al., 2017). To evaluate whether complexity and tolerance correlate in macaque social

organization, we calculated the complexity indices in two species of contrasting social relationships: tolerant Tonkean macaques and intolerant rhesus macaques.

2.5.1 Diversity

Individuals display different behaviors and statuses in social groups according to their age and sex, and therefore demographic categories can be used as types to assess social diversity (Blumstein and Armitage, 1997). To express the uncertainty of systems, possible outcomes should be defined according to the logic of Shannon's entropy. For each variable of interest, the construction of a sample space requires that the distribution of outcome probabilities be expressed in a way meaningful for uncertainty. Based on field data in each species of macaque, we assigned individuals to three age-and-sex categories: adult males, adult females and immatures (Supplementary material). We used these categories as outcomes to define a sample space, where the uncertainty is higher when groups had a more balanced composition of individuals from each category. Calculating relative diversity indices, we obtained h_{vD} = 0.890 and 0.979 in rhesus and Tonkean macaques, respectively (Supplementary material). We used a single variable to estimate the diversity of macaque social systems, so the diversity index D was equal to h_{vD} in each species.

2.5.2. Flexibility

We can use Shannon's entropy to quantify behavioral variations in individuals (Freeberg, 2006; Peckre et al., 2019). Comparative data were available in macaques for two kinds of social events: in the reconciliations that follow conflicts and involve different behavior patterns, and in the occurrences of a specific facial expression, the bared-teeth display, which is observed in different social contexts (Supplementary material). These two kinds of events allow to estimate structural and functional flexibility, respectively. With regard to reconciliation, we differentiated between four categories of behaviors (body contact, vocal signal, facial expression, gesture). The sample space was defined by the proportions of behavior occurrences: the larger the number of behaviors simultaneously occurring in a reconciliation, the higher is the uncertainty of the social encounter. We calculated the relative flexibility indices, and obtained h_{vF} = 0.560 and 0.615 in rhesus and Tonkean macaques, respectively (Supplementary material). With regard to the bared-teeth display, the sample space was composed of five social contexts (affiliation, play, mating, submissive response to aggression, spontaneous submission) as outcomes: the larger the number of contexts of occurrence for this facial expression, the higher is the uncertainty. For the relative flexibility indices, we obtained h_{vF} = 0.354 and 0.569 in rhesus and Tonkean macaques, respectively (Supplementary material). Lastly, we calculated the flexibility index F in each species as the mean of the relative flexibility indices: rhesus macaques F = 0.457, Tonkean macaques F = 0.592.

2.5.3. Combinability

We estimated the uncertainty stemming from relationships between group members based on two kinds of social interactions. We used the distribution of social grooming among individuals at rest to assess the degree of subdivision of the group into subgroups (i.e. modules) as a function of kinship ties; and we used social conflicts by distinguishing between unidirectional conflicts (i.e. including a winner and a loser) and bidirectional conflicts (i.e. both opponents threaten or attack each other, without producing a clear winner) to assess the degree of uncertainty in the outcomes of the interactions. Grooming interactions could be exchanged between close kin partners or non-close kin partners. We reasoned that strong kinship ties could be used to reliably know which are the most frequent partners – corresponding to relatively closed clusters of related partners – , whereas weaker ties make the partner choice less predictable, with less recognizable clusters of related partners. This led to a sample space where the less kin-biased were partner choices, the more they were uncertain. We calculated the relative combinability indices and obtained h_{vC} = 0.548 and 0.983 in rhesus and Tonkean macaques, respectively (Supplementary material). With regard to social conflicts, the sample space was defined by the proportion of aggression displayed by each opponent in pairs of individuals, where the uncertainty was higher when both opponents displayed similar rates of aggression. For the relative combinability indices, we obtained h_{vC} = 0.229 and 0.881 in rhesus and Tonkean macaques, respectively (Supplementary material). Lastly, we calculated the combinability index C in each species as the mean of relative flexibility indices: rhesus macaques C = 0.389, Tonkean macaques C = 0.932.

2.5.4. Complexity

By summing (9) the three indices D, F and C measured in each species, we obtain the following values for the complexity index: 1.74 for rhesus macaques and 2.50 for Tonkean macaques (Fig. 1). This result is consistent with the hypothesis that system complexity increases with social tolerance among macaques. Note that we have used the example of macaque social systems to describe the calculation of the complexity index, but data from a higher number of species would be necessary to test whether the indices measured in different kinds of species are statistically different.

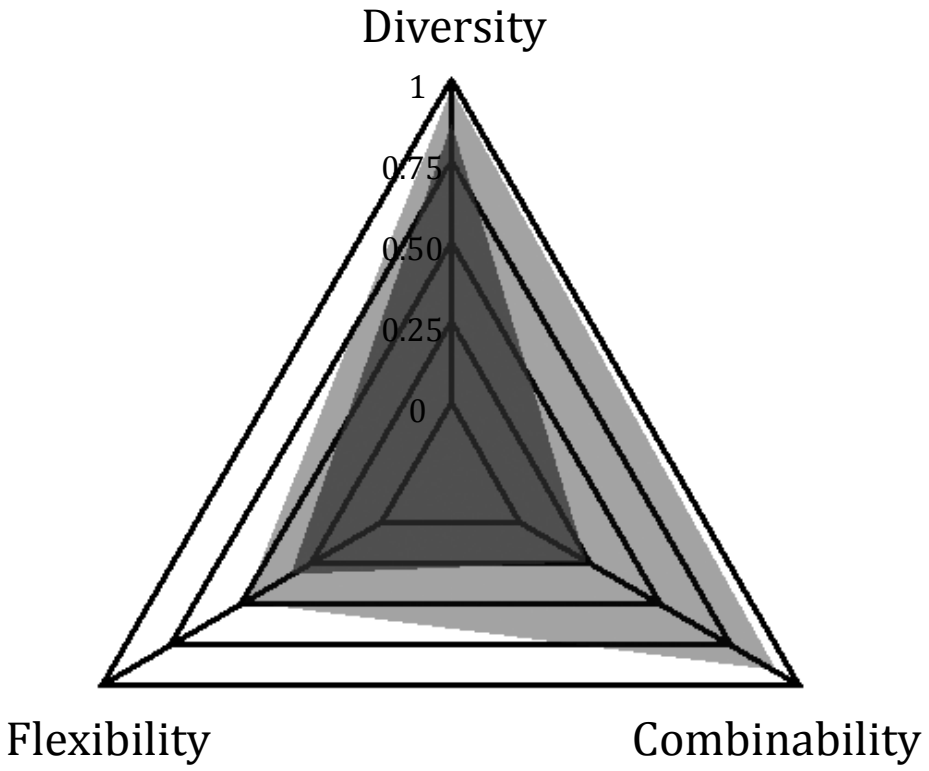


Fig. 1. Radar plot comparing indices in rhesus (dark grey) and Tonkean macaques (light grey). Each spoke represents an index. The plot reads from the center outward along each spoke. Scores are shown on concentric triangles beginning at 0 (center) and increasing to 1 (outer triangle). We can see from the figure the relative contribution of each index to the discrepancy found between species regarding the complexity of their social systems.

3. Discussion

Research has long focused on single features of complexity rather than acknowledging its multidimensional nature (Pollard and Blumstein, 2012; Feng and Bailey, 2018; Kappeler, 2019; Peckre et al et al., 2019). Diversity, flexibility and combinability each capture a part of complexity. By integrating their measurements we may also encompass the whole complexity of biological and cultural systems. These indices based on Shannon's uncertainty differ from previous measurements by several aspects.

First, we doe not make direct use of the number of parts of a system to estimate complexity. Common sense considers a large number of elements as a main characteristic of complex systems, the number of basic components of a systems is a rather crude proxy. Few people

would use the number of cells to compare the complexity of a fly with those of large sponge, and it is well known that the variation in the genome size among organisms does not have simple relationships with the number of coding genes or levels of phenotypic organization (Maynard Smith and Szathmáry, 1995; Gregory, 2001). Another example comes from testing the hypothesis that an increase in social complexity drove the evolution of enhanced cognitive abilities through the evolution of species. After decades of research, the issue has yet to be resolved, due in part to the fact that social complexity was approximated by the number of individuals per group, and cognitive performances by brain size (Powell et al., 2017; Kappeler, 2019). However, it is not excluded that considering the number can be relevant to studying the complexity of a specific system. It should be asked whether this number contributes to the uncertainty of this system. If an increase in the number of elements of a system results in greater uncertainty in that system, then considering the number is relevant in the complexity framework To include the number of elements of the system in the complexity index, a conversion of the number into an entropy value is possible.

In general terms, Shannon's index includes the number of types, it should be noted that it indirectly takes the number of elements into account. In the study of societies, for instance, differentiating between familiar and non-familiar partners has little relevance in small groups, while several categories of familiarity can be distinguished as the size of the groups increases. More generally, the amount of types tends to increase with the number of elements of a system (e.g., Bell and Mooers, 1997; Carroll, 2001; Ferguson-Gow et al., 2014).

The inclusion of flexibility is a second distinctiveness of our proposal. To date, flexibility has been missing from works aiming to measure complexity. Yet it is present at all levels of organisms and organizations; it conditions their adaptation, robustness, and reproduction (West-Eberhard, 2003). It is hypothesized, for example, that flexible social systems have evolved as a response to unpredictable environments in animals (Schradin et al., 2018). More generally, living beings are capable of learning, which adds a further layer of flexibility, the importance of which varies to a considerable extent depending upon the species. It may also be worth remembering that the ability to learn from others forms the basis upon which cultural systems rest and which themselves are rich in changes and innovations (Laland, 2017). This makes it essential to account for a significant number of flexibility variables in order to measure the complexity of systems.

Many authors have distinguished between diversity, measured by the number of types, and modularity, measured by the number of parts. As these two kinds of variables are often considered separately, however, the paradox is that they can be one and the same thing. For instance, the number of cell types in organisms and the number of castes in insect societies may be alternatively counted as diversity (number of specialized types) or modularity (number of

specialized parts) (McShea, 1996; Bell and Mooers, 1997; Ferguson-Gow et al., 2014). The issue originates from the definition of the subunits making up a system. Any subunit can be decomposed into more basic subunits, and therefore the decision of which level to focus the analysis becomes somewhat arbitrary. By requiring that diversity and combinability be taken into account simultaneously, the tripartite complexity index obliges that a differentiation be made between the basic components of a system and their number of categories on one side, and the number of modular parts or nested levels on the other. This is a third characteristic of the index. Moreover, it needs to specify the basic components of the systems under consideration, thereby avoiding confusion between levels. When studying the complexity of animal communication, for instance, the flexibility of signals emitted by individuals should not be mixed with the diversity of repertoires which typically applies to populations or species.

Lastly, our complexity indices go beyond a mere empirical denumbering of parts. Building upon information theory, they enable the comparison of different systems by explicitly quantifying complexity levels in terms of uncertainty. It should be emphasized that it may be useful to compare not only systems based on the tripartite complexity index, but also dimension per dimension. Some systems may differ in some dimensions and be similar in others. There is still room for improvement since each complexity dimension may be measured in multiple ways. An index is as good as the data on which it is based, so it is advisable to measure each dimension by as many variables as possible. At present, it is difficult to find in the literature the data needed to calculate the complexity index for living organisms and social organizations. Hopefully, the present proposal will encourage research programs that aim to measure the variables needed to compare the complexity levels of systems belonging to different realms.

Supplementary material

Calculation of indices for macaque social systems

Diversity

We use demographic data from non-provisioned, free-ranging groups of rhesus (Edwin and Chopra 1984; Kumar et al. 2013) and Tonkean macaques (Pombo et al. 2004; Riley 2007). We first calculate the proportion of adult males, adult females and immatures in each group, then the mean proportion of each demographic category in each species (Table 1). From these numbers, we calculate Shannon's entropy H and the relative diversity index h_{vD} for each species (Table 1).

Flexibility

We measure two flexibility indices. The first index deals with the affiliative behaviors that occur between previous opponents during reconciliations following conflicts (Aureli et al. 2002). We use data from Demaria and Thierry (2001, Table 1). Reconciliations involve different behavior patterns that be classified under four main categories of behaviors (body contact, vocal signal, facial expression, gesture). To choose a sample space, we consider that uncertainty is higher when several behaviors – and in particular 4 behaviors – simultaneously occur.[1] In this case, we expect a more even distribution in the behavior occurrences. We thus calculate the occurrence proportion of behaviors for each reconciliation event; following a Boolean approach, each of the possibly occurring behaviors is represented as a binary variable (counted 1 when present, 0 when absent), divided by the total number of occurring behaviors, with the sum of these probabilities being 1. For example, if an individual contacts another and emits a call, the probabilities associated with each of these behaviors is 0.5, while they are 0 for visual and gestural displays. We use probability values to calculate a mean probability for each category of behavior (Table 1). In a last step, we calculate Shannon's entropy H, then the relative flexibility index h_{vF} in each species of macaque (Table 1).

Table 1. Values calculated from the data: occurrence proportions, H and H_v

	rhesus macaques	Tonkean macaques
Diversity: demographical categories		
Adult male	0.138	0.284
Adult female	0.336	0.280
Immature	0.526	0.436
H	1.41	1.55
h_{vD}	0.890	0.979
Flexibility: reconciliation patterns		
Body contact	0.771	0.711
Vocal signal	0.046	0.031
Facial expression	0.108	0.188
Gesture	0.075	0.071
H	1.12	1.23
h_{vF}	0.560	0.615
Flexibility: contexts of the bared-teeth display		
Affiliation	0	0.635
Play	0	0.180
Mating	0	0.151
Response to aggression	0.331	0.026
Spontaneous submission	0.670	0.010
H	0.915	1.47
h_{vF}	0.354	0.569
Combinability: grooming partners		
Close kin	0.873	0.424
Non-close kin	0.127	0.576
H	0.548	0.983
h_{vC}	0.548	0.983
Combinability: social conflicts		
Most frequent aggressor	0.963	0.700
Least frequent aggressor	0.037	0.300
H	0.229	0.881
h_{vC}	0.229	0.881

A second measurement of flexibility is based on the contexts of occurrence of a facial expression, the silent bared-teeth display, which can convey an affinitive or a submissive display according to social situations and species (Preuschoft and van Hooff 1997). We define five contexts for the bared-teeth display: affiliation, play, mating, submissive response to aggression, spontaneous submission. We use the data provided by de Waal and Luttrell (1985, Fig. 2) and Preuschoft (1995) to obtain the proportion of display occurrences in each context, and calculate *H* then h_{vF} in each species of macaque (Table 1).

Combinability

To estimate the degree of uncertainty in social relations, we use data from one group of rhesus macaques and one group of Tonkean macaques (C. Desportes and B. Thierry, unpublished data; Demaria and Thierry 2001; Rebout et al. 2017).

With regard to the influence of maternal kinship ties on the distribution of social grooming between females at least 5 years old, we use data collected using scan sampling at intervals of 30 minutes. We distinguish between close kin (closely-related kin: mother/daughter, grand-mother/grand-daughter, sisters) and non-close kin (distantly-related or unrelated partners). To get the proportion of grooming exchanged between close kin versus non-close kin for each female, we calculate her adjusted numbers of grooming scans (numbers of scans in which she was involved in grooming divided by the number of potential partners) with each of these categories of partners, and divide each of these adjusted numbers by their sum. We then calculate the mean proportions of grooming with close kin and non-close kin in each group (Table 1). In a last step, we calculate Shannon's entropy *H*, and then the relative combinability index h_{vC} in each species of macaque (Table 1).

A second estimate of combinability is based on the uncertainty in the outcome of social conflicts. We use data collected using all occurrence sampling in subjects that are at least 5 years old. To choose a sample space, we consider that uncertainty is higher when both opponent have similar rates of aggression toward each other. We use the proportion of aggression performed by each opponent as the sample space.[2] From the conflicts occurring in each pair, we calculate the proportion of aggression by each opponent (for unidirectional conflicts we count 1 for the aggressor and 0 for the aggressee, for bidirectional conflicts, we count 0.5 for each opponent). We remove pairs where no conflict occurred. As we are interested by the magnitude of deviation between both opponents, we distinguish in each pair between the most frequent aggressor (i.e., opponent responsible for the higher proportion of aggression) and the less frequent aggressor (i.e., opponent displaying a lower proportion of aggression). We calculate a mean proportion for each kind of opponent in each group, and we calculate *H* and then h_{vC} for these values in each species of macaque (Table 1).

[1] It would be wrong to merely sum the occurrences of the combinations '1 behavior', '2 behaviors', '3 behaviors' and '4 behaviors' because in extreme cases where animals would mainly use four behaviors simultaneously this would lead to low values of *H* (meaning low uncertainty).

[2]It is not possible to sum the occurrence proportions of 'unidirectional conflicts' and 'bidirectional conflicts' because in extreme cases with mostly bidirectional conflicts that would lead to a low value of *H* (meaning low uncertainty).

References

Edwin CJ, Chopra SRK (1984) Group characteristics of *Macaca mulatta* inhabiting submontane and montane forests of the Indian subcontinent: a comparative review. In: ML Roonwal, SM Mohnot, NS Rathore (eds) Current primate researches. Jodhpur University, Jodhpur, pp 307–313

Pombo, AR, Waltert M, Mansjoer SS, Mardiastuti A, Mühlenberg M (2004) Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: G Gerold, M Fremerey, E Guhardja (eds) Land use, nature conservation, and the stability of rainforest margins in southeast Asia. Springer, Berlin, pp 313–325

Riley EP (2007) Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. Int J Primatol 28:107–133

Kumar R, Sinha A, Radhakrishna S (2013) Comparative demography of two commensal macaques in India: implications for population status and conservation. Folia Primatol 84:384–393

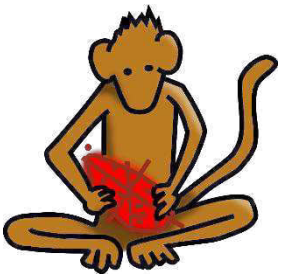
Aureli F, Cords M, van Schaik CP (2002) Conflict resolution following aggression in gregarious animals: a predictive framework. Anim Behav 64:325–343

Demaria C, Thierry B (2001) A comparative study of reconciliation in rhesus and Tonkean macaques. Behaviour 138:397–410

Preuschoft S, van Hooff JARAM (1997) The social function of 'smile' and 'laughter': variations across primate species and societies. In: U Segerstråle, P Molnár (eds) Nonverbal communication: where nature meets culture. Lawrence Erlbaum Associates, Hillsdale, NJ, pp 171–190

de Waal FBM, Luttrell LM (1985) The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. Am J Primatol 9:73–85

Preuschoft S (1995) 'Laughter' and 'smiling' in macaques: an evolutionary perspective. PhD thesis, Rijksuniversiteit Utrecht, Utrecht



CHAPTER 4
Constructing a frame of reference to compare clusters

Constructing a frame of reference to compare clusters

1. Introduction

One of the greatest challenges of the current thesis was to find appropriate methods to compare vocal diversity and vocal flexibility in the vocal repertoire of macaques. As raised by Fischer and colleagues (2017), the major technical problem is to identify the relevant number of call categories in a graded system due to variations within categories and between categories. Moreover, subjective classifications are no longer accepted and the use of algorithm-based methods, such as unsupervised clustering, is recommended (Deecke and Janik 2006; Pozzi et al. 2010). Thus, I turned to unsupervised machine learning, seeking not only to objectively measure vocal diversity and flexibility, but also to compare these values between different species. However, no guideline exists regarding such methods, and, to perform the comparative analysis, I had to develop my own framework of standardisation procedures (which is detailed in this chapter). In addition, it should be noted that the challenges associated with comparing diversity and flexibility between different groups extend well beyond the field of behavioural studies.

Nowadays, science and technology are generating an ever-increasing amount of data. Analysing data becomes very hard to perform for a single mind. Therefore, computer assistance is needed, making unsupervised mining methods required to discover trends in huge and multidimensional datasets. Among unsupervised methods, ‘cluster analyses’ allows to group elements (i.e., observations, data points) according to their similarity from a multivariable point of view. Hence, based on selected variables, cluster analysis classifies elements into several categories or clusters. Cluster analyses have countless applications in machine learning, image processing, marketing, bioinformatics, health science, ecology, etc. Two frequently used methods are hierarchical clustering, which progressively aggregates data to classify elements into successive subcategories, and K-means clustering, which requires specifying the optimal number of categories (Everitt et al. 2011; Hennig et al. 2016). Another method, model-based clustering, considers that the data come from a mixture distribution of several clusters. During model-based clustering, each model is assigned with a fixed number of clusters. Then, the

probability of one element to belong to each cluster is calculated based on cluster's distribution. Finally, several models are executed and the best model (i.e., the one with the optimal number of categories) is selected. One type of selection can be based on the Bayesian information criterion (BIC) (Banfield and Raftery 1993; McNicholas 2016).

Cluster analyses are generally used to find clusters within a single dataset and are not intended to compare datasets. Their algorithms reveal clusters by grouping elements based on the evaluation of their relative distances. As relative distances depend on the distribution of variables describing each dataset, clusters are specific to each set of datasets. Therefore, different sets of clusters are not directly comparable since the resulting distances are not measured on a common scale. For example, a cluster drawn from one analysis may actually correspond to a subcluster drawn from another analysis. This may be illustrated by two examples.

In cell biology, the different cell categories of organs and tissues can be identified from their transcriptomic data, i.e., protein and mRNA expression patterns (Alberts et al. 2019). Cluster analyses may help determining the number of cell categories for each organ in mice (Schaum et al. 2018). It would be worth knowing whether two individuals or two strains display the same number of cell categories and subcategories (clusters and subclusters). However, individuals or strains differ in their genomes and transcriptomes. How could the results of cluster analyses conducted on different datasets be compared in an unbiased manner?

The second example can be taken from the field of psychopathology. Cluster analyses are used to identify major categories (clusters) of mental disorders based on the multiple behavioural and psychological symptoms recorded in patients (Everitt and Landau 1998; Sheets and Craighead 2007). But how do we proceed if we want to know whether the same major categories of disorders occur in societies of different cultures? It is acknowledged that some mental disorders can be relevant in one culture and almost non-existent in another (Becker and Kleinman 2000; Tseng 2001). As categories may vary from one dataset to another, cross-cultural comparisons are problematic. How to determine whether two categories of disorders revealed by separate cluster analyses in different cultures are actually homologous, or that one is a major category and the other a subcategory of another major category?

Here, I propose a standardisation procedure to compare the results of cluster analyses performed on separate datasets. This procedure is based on the creation of a frame of reference using standardised variables.

2. Standardisation procedure

When comparing the results of cluster analyses performed on different datasets, the problem is the same regardless of the clustering method used: the scale of distances between elements may vary from one dataset to another. We need to build a frame of reference to solve this problem.

Defining a space in which a cluster analysis is applied requires choosing variables that are relevant to differentiate clusters in subjects. Each variable can be considered as a distinct dimension, and all variables taken together define a multidimensional space. It is a space where distances between elements measure the similarity between them. Cluster analyses use these distances to cluster elements. The shorter the distance between two elements, the greater the degree of similarity between them and the greater the probability that these elements will be classified in the same cluster. However, if the variables have different scales, their effects on clustering will not be the same. If some variables have an especially large value or great variability, such variables can have a significant impact on the results of the analysis. In extreme cases, a single variable may be the only factor determining distances between elements. For example, if an analyst intends to group people based on their weight in kilograms and height in meters, a difference of one kilogram may be not as significant as a difference of one metre. These two variables have different scales, and distances will be influenced to a greater extent by the variable weight. Therefore, it is essential to standardise each variable before applying a clustering method, as it allows the variability of the dataset to be controlled. This makes the variables comparable and improves the accuracy of clustering algorithms (Mohamad and Usman 2013). One data standardisation type is to transform the variables, so that they have a mean of zero and a standard deviation of one (Mohamad and Usman 2013). For this transformation, we standardise the variables using the following formula:

$$x'_{ij} = \frac{x_{ij} - \mu_j}{\sigma_j}$$

where μ_j and σ_j are, respectively, the mean and standard deviation for the j^{th} variable in the dataset, x_{ij} is the i^{th} element for the j^{th} variable, and x'_{ij} is the standardised value of the i^{th} element for the j^{th} variable

When applying this standardisation to a single dataset, there is no issue. This creates a space specific to this single dataset where the scale of each dimension (variable) in the multidimensional space is comparable. If we want to compare different datasets with the same variables, however, the problem is that the variables may have different distributions. These variables may have different values and differ widely in their means and variances, which alters the standardisation process. In this case, distances and clustering outputs can be affected. Distances may not be comparable from one dataset to another and the same applies to clustering

outputs. To compare the different clustering outputs, we have to use a common frame of reference, i.e., a common space. For this reason, we propose to use all elements of the different datasets for each variable and, then, to scale these variables according to the combined dataset. This way, the cluster analyses performed on each dataset are placed in the same common space, and the elements will be standardised for all datasets. This means that distances are now comparable, allowing the outputs of clustering applied to different datasets to be compared.

2.1. Reducing the number of spatial dimensions

Clustering can be directly applied to variables following the standardisation procedure. However, other methods such as Principal Component Analyses (PCA) (Jolliffe 2002; Abdi and Williams 2010; Naik 2017) can be applied in between-variable standardisation and clustering methods. PCA are indeed frequently used to reduce the dimensionality of datasets containing many variables. They summarise the information in the dataset by creating a space with a reduced number of dimensions (Jolliffe 2002; Abdi and Williams 2010), which removes factors correlations that might influence clustering. A PCA step preceding a cluster analysis can also be used to remove noise, which leads to a more stable clustering (Ben-Hur and Guyon 2003; Kassambara 2017). This process results in spaces that are defined by the PCA dimensions (principal components) rather than the standardised variables.

2.2. Clustering procedure

Once the spaces have been built and cluster analyses completed, the final step is to compare the outputs of several cluster analyses using statistical methods. Depending on the question to be answered, it is possible to compare the optimal number of clusters expressing the diversity of the dataset, the degree of overlap between clusters, or even distances between clusters' centroids (means). Additional tests can be used to compare the number of variables needed to describe a set of clusters. Using clusters as a response variable, a discriminant function analysis or a random forest analysis can quantify the number of informative and non-informative variables in the dataset.

3. Assessing diversity and flexibility

As the vocal repertoire of macaques is graded, it is necessary to choose an appropriate clustering method. To assess the diversity and flexibility of their vocal signals, I will use soft clustering methods such as model-based and fuzzy clustering.

3.1. Vocal diversity

My aim was to quantify the number of clusters structuring the dataset as a measurement of the diversity. The larger the number of clusters, the greater the vocal diversity. I decided to use model-based clustering, a probability-based approach (Banfield and Raftery 1993; McNicholas 2016) that includes a Gaussian mixture model (GMM) based clustering approach (Goeffrey and Peel 2000; Everitt 2014; McNicholas 2016). In short, GMM assumes clusters can be built based on a finite mixture of probability distributions. Therefore, GMM allows each group to be described by a different volume, shape, and orientation. Distribution parameters needs to be computed, which was done using an expectation maximisation (EM) algorithm. Then, the best model was selected based on the BIC) score. Although most clustering algorithms consider that every point is assigned to a single cluster, leading to a black and white system, GMM are able to manage a system with different grayscales and, therefore, account for gradation, which is particularly well suited for the study of graded repertoires. This allowed me to consider the probabilities of soft clustering algorithms as a way to determine the degree of gradation between clusters, and conclude about flexibility.

3.2. Vocal flexibility

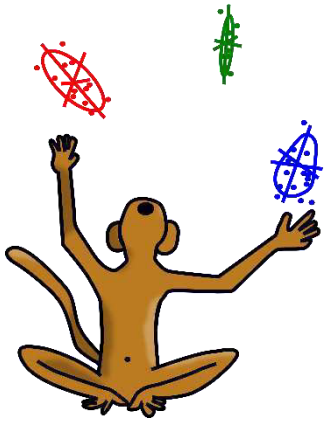
Vocal repertoires are considered to be graded systems where there is no clear boundary between call types, i.e., there is a continuum in the acoustic structures (Hammerschmidt and Fischer, 1998; Wadewitz et al., 2015). Therefore, hard clustering methods (K-mean, hierarchical clustering) are not appropriate to capture the gradation between call types. To overcome this limitation, soft clustering methods can be used (e.g., GMM). However, due to the varying shape of GMM's cluster types (variation in cluster shape, volume and orientation), it is not optimal for comparison between species. Another soft clustering method can describe systems with a continuum. Fischer and colleagues have proposed a procedure for quantifying the degree of gradation in a vocal repertoire using a soft clustering algorithm called fuzzy clustering algorithm (Wadewitz et al. 2015; Fischer et al. 2017b). Fuzzy clustering is based on the principle that a single point can be a member of several clusters. This imperfect membership is assigned a value between 0 (does not represent the cluster at all) and 1 (perfectly represents the cluster). Intermediate membership is classified as intermediate between clusters. The more intermediates there are, the more graded the repertoire. Fisher and colleagues (2017b) proposed to better define the graded structure. They suggest to discriminate between typical calls, i.e., calls with a high probability to belong to one given cluster, and atypical calls, i.e., calls having a low probability of belonging to this cluster. However, this approach leads to the definition of discrete thresholds to differentiate between typical and atypical calls, although the purpose is specifically to describe the graded nature of a repertoire. Lastly, the use of typicality does not

allow to quantify the degree of gradation of the whole repertoire. Therefore, I propose a new approach that permits to calculate the degree of gradation of an entire vocal repertoire, making it possible to compare the repertoires of different species. My approach has the advantage of not basing the conclusion on a discrete threshold. It is directly based on the probability distribution from soft clustering algorithms, such as fuzzy clustering, but also model-based clustering.

In order to study the fuzzy membership of intermediate calls in a continuous manner, I decided to use the Shannon's entropy index as a quantifier of gradation. Shannon's approach has the advantages of a solid mathematical foundation and to link the properties of graded repertoires to variables derived from complexity theory, which is precisely what Fischer and colleagues (2017b) have suggested. Briefly, the Shannon entropy index (Shannon 1948) assigns higher values when the probabilities of membership are evenly distributed and lower values when the probability of membership favours one group. Consequently, Shannon's index is particularly well suited to quantify the degree of gradation in a fuzzy clustering system. Thus, I propose to use the membership probabilities for each element of a system, then to compute the entropy of each element and, finally, to calculate the mean entropy as an estimation of the degree of gradation of a system. It should be noted that the degree of gradation may be influenced by the number of clusters. As a solution, I will quantify the degree of gradation for different numbers of cluster, i.e., by varying the number of clusters from the minimum and maximum optimal number of clusters determined in the estimation of diversity.

4. Conclusion

The use of a common frame of reference solves two different issues. The first one is the problem of scale. The construction of a common space assigns the distances between elements to the same scale. The purpose of a cluster analysis is precisely to group elements on the basis of these distances. If distances are not comparable, the results of the analysis are not comparable either. The second issue is the comparative problem. When distances are not comparable, we are at risk of comparing the main clusters of one dataset with the subclusters of another dataset. Building a common space should allow to compare different datasets by promoting homologous comparisons. The use of soft clustering algorithm is particularly well suited for the study of graded systems. The use of both model-based and fuzzy clustering methods should allow to quantify and compare the vocal diversity and vocal flexibility between several species. These methods should have numerous applications in various fields, going beyond the field of animal communication. In the following chapters, I will apply them to the comparative study of vocal signals in macaques.



CHAPTER 5
Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

Abstract

We tested the social complexity hypothesis for communicative complexity, which posits that animals living in complex social environments should use complex communication systems. We focused on two components of vocal complexity: vocal diversity, i.e. the number of categories of calls, and vocal flexibility, i.e. the degree of gradation between categories of calls. We studied these two components in animals with varying levels of uncertainty (i.e. complexity) in social interactions and social tolerance: the higher the degree of tolerance, the higher the degree of uncertainty. We compared the acoustic structure of vocal signals in several groups of macaques belonging to four species: two intolerant species, Japanese and rhesus macaques, and two tolerant species, Tonkean and crested macaques. We recorded the vocalizations emitted by adult females in affiliative, agonistic, and neutral contexts. We analysed the following acoustic variables: call duration, entropy, and time and frequency energy quantiles. The results showed that tolerant macaques displayed higher levels of vocal diversity and flexibility than intolerant macaques in the context where the stakes were highest, i.e. the agonistic context. The extent of contrasts between tolerant and intolerant macaques was less pronounced in the affiliative context, and absent in the neutral context. It appears that species experiencing more uncertain social interactions were also those with greater vocal diversity and flexibility. This supports the social complexity hypothesis and highlight the role of the context. Higher levels of vocal complexity should provide tolerant macaques with a greater richness of communications signals, which would help them managing undecided social events, especially in competitive situations.

Keywords

Social complexity, diversity, flexibility, communication, acoustics, non-human primates.

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Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

1. Introduction

When looking for the determinants of social evolution in animals, two main types of factors can be distinguished, environmental and structural. Understanding how adaptation to environmental factors shapes social behaviour has attracted a great deal of research, and is, in fact, the main objective of the field of behavioural ecology (Danchin et al. 2008; Davies et al. 2012). In comparison, the role of structural constraints in biology has long been a controversial issue (Gould and Lewontin 1979; Maynard Smith et al. 1985), and much less effort has been devoted to studying how they channel social organizations (Thierry 2013). Although the definition of structural constraints itself has been problematic for some time, they can be actually defined as processes that limit the response of phenotypic traits to the selective action of ecological factors (Antonovics and van Tienderen 1991; Schlichting and Pigliucci 1998). These constraints arise from the existence of functional relationships that link phenotypic traits or from passive interconnections that have occurred over the course of evolutionary history, and keep them in an entrenched state (Wimsatt and Schank 2004; Brooks and McLennan 2013; Thierry 2013).

According to the *social complexity hypothesis for communicative complexity*, there is a functional relationship between patterns of communication and patterns of social organization: animals living in complex social environments should use complex communication systems because a complex social life increases the need to discriminate individuals, express a wide range of emotional states, and convey a broad variety of messages related to different goals and contexts (Freeberg, Dunbar, & Ord, 2012; Pollard & Blumstein, 2012; Peckre et al., 2019b). Although the social complexity hypothesis applies to communicative signals in general, most of the current evidence comes from the study of vocal communication (Freeberg et al. 2012a). The correlations found between the amount of information or the size of vocal repertoire on one side, and the size of social groups (McComb and Semple 2005; Freeberg 2006b; Wilkinson et al. 2019) or the number of categories of individuals on the other side (Blumstein and Armitage 1997; Pollard and Blumstein 2012) are in line with this hypothesis. However, there are problems with the definition and measurement of both social and vocal complexity.

There is no consensus on measures of the complexity of social systems (Chu et al. 2003; Freeberg et al. 2012a; Bergman and Beehner 2015; Fischer et al. 2017a; Kappeler 2019a). The number of individuals in a social unit, as well as the number of categories of individuals or social interactions, have long been used as indicators of complexity (Dunbar, 2012; Freeberg, 2006a; Lehmann & Dunbar, 2009; Blumstein & Armitage, 1997; Pollard & Blumstein, 2012; Freeberg et al., 2012). More recently, authors have focused on the number of social relationships or associations between group members (Bergman & Beehner, 2015; Fischer, Farnworth, et al., 2017; Weiss, Franks, Croft, & Whitehead, 2018/2019). Numbering the

components of social systems may provide good proxies for assessing their diversity, but diversity is only part of complexity, it is far from exhausting it (Chapter 3), which undermines the evaluation of the social complexity hypothesis.

A similar problem hinders the measurement of the complexity of vocal communication (Fischer et al. 2017b). Authors generally assume that the greater the number of call types, the higher the level of vocal complexity (McComb and Semple 2005; Freeberg 2006b; Gustison et al. 2012; Maciej et al. 2013). What is considered again is the diversity of communication signals rather than the complexity of the entire vocal system. Moreover, there is no agreement on how to identify the types of calls, and therefore the size of a species' communicative repertoire (Fischer et al. 2017b). The task is especially tricky when repertoires are graded, that is, when there is a gradual transition from one acoustic structure into another (Marler and Tamura 1964; Fischer et al. 2017b), as reported in species such as primates (Hauser 1996; Marge and Fischer 2004). Some have proposed abandoning the idea of counting the number of calls to quantify vocal complexity, and instead using the degree of gradation of repertoires (Wadewitz et al. 2015; Fischer et al. 2017b), i.e. flexibility in the acoustic structure of vocal signals. Since diversity and flexibility represent two different components of complexity, however, it seems that the best solution is to measure the two separately (Chapter 1).

The ability to produce uncertainty appears to be the most important characteristic of complex systems (McDaniel and Driebe 2005; Schuster 2016). Information theory (Shannon, 1948) provides a means to quantify diversity and flexibility in terms of uncertainty (Chapter 1). The social complexity hypothesis can, therefore, be tested by comparing the diversity and flexibility of communication in species with varying levels of uncertainty in their social relationships. These species must be close enough to allow for homologous comparison from the point of view of both social relations and communication signals. In this respect, the genus *Macaca* offers a model that meets these requirements. Macaque species exhibit wide variations in their degree of social tolerance, related to different levels of uncertainty in the outcome of their agonistic interactions (Dobson, 2012; Zannella, Stanyon, & Palagi, 2017). In the most intolerant species, social conflicts generally have clear consequences: in Japanese macaques (*Macaca fuscata*) and rhesus macaques (*M. mulatta*), for example, the recipient of aggression flees or submits in nine out of ten cases among unrelated females (Thierry et al. 2008). By contrast, in more tolerant species the recipient of the aggression frequently protests or counter-attacks: in Tonkean macaques (*M. tonkeana*) and crested macaques (*M. nigra*), 68.0 and 45.4% of conflicts among unrelated females, respectively, remain undecided, with no clear winners and losers (Thierry et al. 2008). Since open contests can expose animals to injury risks and have consequences on resource competition, individuals should need more information to deal with the many potential outcomes of uncertain situations. This is not necessarily so in other circumstances, and it would, therefore, be valuable to compare contexts (Freeberg et al. 2012).

Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

In the context of affiliative interactions or in neutral situations – i.e. when there are no direct interactions between groupmates – no significant differences between species should be expected in the complexity of their communication systems.

The interspecific variations reported in the agonistic patterns of macaques covary with other components of their social style such as hierarchical steepness, degree of nepotism, reconciliation rates, or range of facial displays; for example, dominance and kinship relations have stronger influence on individual behaviours in intolerant macaques compared with tolerant macaques, and the latter reconcile more often and have a greater number of facial displays than the former (Thierry 2007; Dobson 2012; Balasubramaniam et al. 2017). Despite such variations, macaque species share the same basic patterns of organization. All are semi-terrestrial primates living in multimale-multifemale groups; males disperse and females remain in their natal group where they constitute matrilines, i.e. subgroups of relatives linked by maternal descent (Thierry 2007). While no association has been found so far between the contrasting social styles of macaque species and the ecological conditions in which they have evolved, it appears that social styles consistently vary with phylogeny: closely related species are more similar than those that are distant (Ménard 2004; Thierry 2013; Balasubramaniam et al. 2017).

In this study, we compared the vocal signals of two tolerant species (Tonkean & crested macaques) and two intolerant species (Japanese & rhesus macaques), based on three main variables (acoustic structure, diversity, flexibility) in three different social contexts (agonistic, affiliative, and neutral). Like the other species of macaque, they use a graded repertoire of vocalizations (Rowell & Hinde 1962; Green 1975; Masataka & Thierry 1993; Gouzoules & Gouzoules 2000; Panggur 2013). They are mainly frugivorous and their primary habitat is the forest, with the exception of rhesus macaques which occur in a variety of habitats, from forests to arid lands or regions of human settlement (Ménard 2004). Both Tonkean and crested macaques live on different parts of Sulawesi island, Indonesia, they belong to the oldest macaque lineage (Fooden 1980). Japanese and rhesus macaques live in Japan and mainland southern Asia, respectively, and both belong to a more recent lineage (Delson 1980; Fooden 1980). The two lineages separated about five million years ago (Tosi et al. 2003; Ziegler et al. 2007). In comparison, the divergence between Tonkean and crested macaques on one side, and Japanese and rhesus macaques on the other side, is much more recent. It is estimated to have occurred almost one million years ago or less (Purvis 1995; Morales and Melnick 1998; Tosi et al. 2003).

We tested the predictions of three different hypotheses: (1) *Null hypothesis*: We should find no significant difference in the calls of tolerant and intolerant species regardless of variables and contexts; (2) *Phylogenetic hypothesis*: Greater similarity should occur in more closely related species, so we should find more differences between Tonkean and crested macaques on

the one hand, and Japanese and rhesus macaques on the other, than within each of these species pairs, for any variable and regardless of the social context; (3) *Complexity hypothesis*: Greater uncertainty in the social interactions of tolerant species compared to intolerant species should lead to greater vocal diversity and flexibility in the former species than in the latter, while no significant differences should be found regarding the acoustic distances of calls. In addition, differences in diversity and flexibility should vary across social contexts: they should be strong in the agonistic context, and weak in the neutral and affiliative contexts.

2. Methods

2.1. Subjects and living conditions

We made behavioural observations and acoustic recordings in 29 adult females from two groups of Japanese macaques, 16 adult females from two groups of rhesus macaques, 13 adult females from four groups of Tonkean macaques, and 51 adult females from two groups of crested macaques. We focused on adult females because they are the most represented age-and-sex category in macaque social groups, and also the most active contributors in vocal communication (Lemasson et al. 2013). Japanese, rhesus and Tonkean macaque females were captive-born and at least five years old. Crested macaques were studied in nature, and the age of the subjects was assessed according to their reproductive history since 2006 (Macaca Nigra Project, www.macaca-nigra.org), their body size, the shape of their nipples, and the presence of old physical injuries. The composition of groups is given in Table 1.

The groups of Japanese macaques (Ft, Fw) were housed in two enclosures of 960 and 4,600 m², respectively, at the Primate Research Institute in Inuyama, Japan (Arlet et al. 2015). The groups of rhesus macaques (Ma, Mb) were housed in two 210-m² enclosures at the Biomedical Primate Research Center in Rijswijk, The Netherlands (De Marco et al. 2019). One group of Tonkean macaques (Tb) was housed at the Orangerie Zoo in Strasbourg, France, in a 120-m² enclosure, and the other three groups (Tc, Td, Te) were housed at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy, in 500-m² enclosures (De Marco et al. 2019). Enclosures were wooded or furnished with perches, ropes, and shelters. Animals were fed commercial monkeys diet pellets, supplemented with fresh fruits and vegetables, and water was available ad libitum. The groups of crested macaques (Npb, Nr1) lived in the Tangkoko Nature Reserve, North Sulawesi, Indonesia (Micheletta et al. 2005). They were not provisioned and inhabit lowland tropical rainforest (Collins et al. 1991; Rosenbaum et al. 1998).

The study complied with the legal requirements and guidelines of the Japanese, Dutch, Italian, and French governments, and followed the ASAB/ABS guidelines for the treatment of animals in behavioural research. For convenience, in what follows we will refer to the Tonkean and crested macaque species as the Tonkean/crested pair, and the Japanese and rhesus macaque species as the Japanese/rhesus pair.

Table 1. Information about groups and subjects (Takahashi et al. 2006; Micheletta et al. 2013; Arlet et al. 2015; De Marco et al. 2019).

Groups	Dates of group foundation and study	Composition of groups	Name and age in years of females[1]
rhesus macaque group Ma	founded in 2004, studied in Jul–Oct 2016	10 adult females, 3 adult males, 22 immatures[2]	*Pip* (14), *But* (13), *Isa* (11), *Nil* (10), *Hoe* (10), *Wie* (9), *Lok* (7), *Aus* (6), *Mon* (5), *Pan* (5)
rhesus macaque group Mb	founded in 2004, studied in Jul–Oct 2016	6 adult females, 1 adult male, 24 immatures	*Tro* (13), *Plo* (12), *Hat* (10), *Jah* (8), *Kwe* (7), *Ymi* (6)
Tonkean macaque group Tb	founded in 1978, studied in Feb–May 2016	4 adult females, 6 adult males, 5 immatures	*Gil* (27), *Gai* (9), *Giu* (9), *Lis* (5)
Tonkean macaque group Tc	founded in 2005, studied in Sept–Dec 2014	4 adult females, 4 adult males, 8 immatures	*Pal* (13), *Sop* (11), *Pam* (8), *Pap* (6)
Tonkean macaque group Td	founded in 2007, studied in Mar–May 2015	3 adult females, 5 adult males, 7 immatures	*Sib* (12), *Tet* (11), *Tan* (11)
Tonkean macaque group Te	founded in 2009, studied in Sept–Dec 2014	2 adult females, 3 adult males, 5 immatures	*Nin* (15), *Nif* (9)
Japanese macaque group Fw	founded in 1974, studied in Mar–Aug 2005	13 adult females, 4 adult males, 10 immatures	*Has* (10), *Min* (6), *Mia* (5), *Nir* (6), *Rek* (14), *Rum* (17), *Mil* (9), *Bel* (5), *Lar* (5), *Som* (18), *Sar* (8), *Jes* (7), *Ren* (20)
Japanese macaque group Ft	founded in 1970/1971, studied in Mar–Jul 2005	16 adult females, 6 adult males, 24 immatures	*Ame* (25), *Iwa* (11), *Kak* (8), Kin (15), Kam (5), Kur (9), *Mor* (22), Shi (10), Sha (8), *Tan* (24), *Tak* (17), *Tsu* (21), *Umi* (19), *Ume* (8), *Yam* (13), *Yuk* (21)
Crested macaque group Nr1	wild population, studied between Sept 2010 & Apr 2011	28 identifiable adult females, 10 adult males, 42 immatures	*Ani*, Adi, Bea, Bas, *Cin*, Dor, Ern, Fen, *Glo*, *Hel*, Isa, *Jos*, Kat, *Leo*, *Min*, *Nur*, Oli, Pol, Qut, *Ros*, *Sup*, *Tut*, Eli, Vod, Wi, Big, Yan, Zoe
Crested macaque group Npb	wild population, studied between Sept 2010 & Apr 2011	23 identifiable adult females, 8 adult males, 29 immatures	*Agn*, *Bia*, *Cic*, Dea, *Eva*, Fio, Geu, Her, Iye, Jan, *Kri*, Lid, Nao, Oma, *Ram*, *Ste*, *Jam*, Mal, Zor, Pap, Val, Tem, Upi

[1]Age at the beginning of data collection. The names of the sampled females are in italics.

[2]Individuals under 5 years of age.

2.2. Data collection

We carried out observations outdoor to ensure the quality of the recordings. Data were collected by A.L. in Japanese macaques (Arlet et al. 2015), N.R. in rhesus macaques, A.D.M., A.S., and N.R. in Tonkean macaques (De Marco et al. 2019), and J.M. in crested macaques (Micheletta et al. 2015) (Table 1). We observed subjects in a predefined random order using focal sampling. Sample duration was 10 min in Japanese, crested macaques, and Tonkean macaques from groups Tc, Td and Te, and 15 min in rhesus macaques and Tonkean macaques from group Tb. This resulted in 6.1 ± 0.16 h of focal sampling per female in Japanese macaques, 12.7 ± 0.7 h in rhesus macaques, 13.6 ± 3.2 h in Tonkean macaques, and 7.8 ± 0.4 in crested macaques.

In Japanese macaques, we recorded vocalizations with a TCD-D100 Sony (Tokyo, Japan) DAT recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and an ECM 672 Sony directional microphone. In rhesus and Tonkean macaques, we used a Marantz (Eindhoven, The Netherlands) PMD 661 recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. In crested macaques, we used partly a high-resolution camera Panasonic (Osaka, Japan) HDC-SD700 linked to a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone, and partly a Marantz (Eindhoven, The Netherlands) PMD 661 (WAV format, sampling frequency: 32 000 Hz, resolution: 16 bits). We collected observational data about the context of call emission with a lavalier microphone connected to the recorder in Japanese, rhesus and Tonkean macaques (at805f, audio-technica, Leeds, United Kingdom vs TCM 160, Meditec, Singapore). In the crested macaques, the observer filmed the focal individual while a field assistant recorded contextual data using a handheld computer; we extracted the audio tracks from the video recordings using the software *FFmpeg* (v 3.4.1).

We distinguished three social contexts: agonistic, affiliative and neutral. They were defined according to the behaviours that could occur in the 3 s before or after the emission of a call or a sequence of calls. A sequence was itself defined as a series of calls separated by a maximum of 3 s. Behavioural units were based on published repertoires for macaques (Altmann, 1962; Fedigan, 1976; Thierry et al., 2000). The agonistic context included aggression (supplantation, lunge, chase, slap, grab, bite, facial threat display) and response to aggression (aggression, avoidance, flight, crouch, submissive facial displays). The affiliative context included affiliative behaviours (approach, sitting in contact, social grooming, social play, grasp, embrace, mount, affiliative facial display). In the neutral context, the caller was not involved in a social interaction.

2.3. Acoustic analysis

We had records for 1368 calls in Japanese macaques, 1026 calls in rhesus macaques, 1210 calls in Tonkean macaques, and 1234 calls in crested macaques. We drew spectrograms using the software Raven Pro v1.4' (Cornell Lab of Ornithology, www.birds.cornell.edu/raven) with a 256 fast Fourier transform length and a Hanning window. With the same software, we measured the following variables: *Duration*: duration from the beginning to the end of a call, in seconds; *Q2 ratio*: ratio between duration that divides a call into two intervals of equal energy and duration, in percentage; *Q1 frequency*: value of the frequency that divides a call into two intervals containing 25% and 75% of the energy, in Hertz; *Q2 frequency*: value of the frequency that divides a call into two intervals of equal energy, in Hertz; *Q3 frequency*: value of the frequency that divides a call into two intervals containing 75% and 25% of the energy, in Hertz; *Wiener's aggregate entropy*: degree of disorder (i.e. noisiness) of the call, which uses the total energy in a frequency bin over the entire call; *Wiener's average entropy*: mean of the mean entropies of the different time slices of a call.

We selected records according to their quality for these variables. We randomly selected no more than three calls per sequence. A sequence was defined as a series of calls separated by a maximum of 3 s. Females with a sample size of less than five calls were excluded from the analysis. We also excluded some specific types of calls that were not present in the samples of all species (alarm calls), or that had no equivalent in all species (œstrus calls, twits, and cackles). Our samples resulted in 434 calls in 24 Japanese macaques (agonistic context: total number of calls, 79 & mean number of calls per female ± *SD*, 3.30 ± 3.77; affiliative context: 94, 3.92 ± 4.16; neutral context: 255, 10.6 ± 5.48), 639 calls in 16 Japanese macaques (agonistic: 118 & 7.38 ± 6.75; affiliative: 59 & 3.69 ± 3.22; neutral: 461 & 28.8 ± 16.0), 700 calls in 13 Tonkean macaques (270 & 20.8 ± 26.3, 226 & 17.4 ± 14.3, 202 & 15.5 ± 8.42), and 696 calls in 19 crested macaques (201 & 10.6 ± 6.61, 297 & 15.6 ± 11.8, 191 & 10.1 ± 7.40).

2.4. Statistical analyses

Statistical analyses were run in *R v 3.5.3* (Core Team 2018). In a first analysis, we tested the differences in acoustic variables between species. In a second analysis, we assessed vocal diversity and compared it across species; we first performed a cluster analysis using an algorithm adapted to the graded repertoire, and then performed a Principal Component Analysis (PCA) before the cluster step. In a third analysis, we quantified the degree of gradation of the repertoire based on assignment probabilities using a second cluster analysis.

2.5.1. Acoustic distances

To test the differences between species in their acoustic variables, we performed discriminant function analyses using the function *lda* of the package *MASS* (Venables and Ripley 2002). Since a discriminant function analysis can be affected by the unit in which predictor variables are measured, we scaled the acoustic variables prior to analysis. As collinearity can bias the results of a linear discriminant analysis (Noes & Movik 2001), we removed acoustic variables so that each Pearson pairwise correlation between acoustic variables was less than 0.7 (Dormann et al. 2012). Therefore, we included the following variables in the discriminant function analysis: duration, Q2 ratio, Q2 frequency, Average entropy. We used the function *PermuteLDA* from the package *multiDimBio* (Samuel V. Scarpino et al. 2013) to assess interspecific differences in acoustic variables that we name *acoustic distances*, which allowed to statistically determine whether the species were at different locations in the multivariate space (Collyer & Adams 2007): it calculated the multivariate distances between the sets of calls of each species in each context, and determined whether they differed significantly using Monte Carlo randomization.

2.5.2. Principal Component Analysis

As individuals were described by multifactorial characteristics, we used Principal Component Analyses (PCA) to reduce the dimensionality of the data set and stabilize cluster results (Ben-Hur and Guyon 2003). In addition, the PCA approach eliminates correlations between factors that can influence clustering. Prior to PCA, and per context for all species, we scaled the seven acoustic variables to obtain a standard deviation of one, and a mean of zero, using the *R base function scale* (Core Team 2018). The PCAs per context were then performed using the *PCA* function of *FactoMineR* package (Lê et al. 2008). We weighted each female according to her number of calls by applying the argument *row.w* of the PCA function to balance the contributions of the different females to the creation of the space. Eventually, we selected the number of dimensions that explained near 95% of the variance of the data.

2.5.3. Vocal diversity

We can measure *vocal diversity* by the number of call types in the repertoire of a species (Freeberg et al. 2012; Peckre et al. 2019). There is more uncertainty in communication when individuals can emit more calls, i.e. when the number of groups of calls is great. We determined the diversity in groups of calls by quantifying the number of clusters that structured the data set. The greater the number of clusters, the greater the vocal diversity. To calculate the optimal number of clusters, we chose to apply Gaussian Mixture models (GMM) based on a clustering

approach (Goeffrey and Peel 2000; Everitt 2014; McNicholas 2016). GMMs assume that the clusters come from a finite mixture of probability distributions, which allows each group to be described with a different volume, shape, and orientation. The distribution parameters must be computed, which has been done by an Expectation maximization (EM) algorithm. The best model was then selected based on the Bayesian Information Criterion (BIC) score. The BIC scoring of a GMM was performed using the function *Mclust* of the package *Mclust* (Scrucca et al. 2016). We have considered only the optimal number of clusters defined by the best model. As we wanted to compare these optimums statistically between each of the species, we used a bootstrap procedure. We ran 100 bootstraps where 80% of the data was sampled per bootstrap.

2.5.4. Vocal flexibility

Uncertainty in communication is greater when individuals have more intermediate calls. We named *vocal flexibility* the degree of gradation between groups of call: the higher it is, the greater is the potential for information transmission (Peckre et al. 2019). We used the probability for a single call to belong to the different clusters to measure the degree of gradation between clusters. Accordingly, we used the soft assignment from a fuzzy clustering algorithm over GMM because we aimed to avoid shape, volume or orientations difference between groups that can affect the likelihood of membership to each cluster. We applied the function *fanny* from the package *cluster* (Martin Maechler et al. 2018). We set the argument membership exponent at 1.2 because it was the higher value – giving a higher degree of fuzziness (Kaufman and Rousseeuw 1990) – that did not lead to convergence issues. Each call was assigned a probability of belonging to each cluster (*N* probabilities per call for *N* clusters). Therefore, if a call had a probability of one to belong to a cluster, and zero to belong to any other clusters, this call was considered as typical of a cluster. On the contrary, if a call had more evenly distributed probabilities, it was considered as an intermediate call between at least two different clusters. The higher the number of intermediates, the higher the degree of gradation between clusters. Hence, to quantify this degree, we could use the Shannon's entropy formula (Shannon 1948): the higher the entropy, the more even the distribution across clusters. We calculated the entropy of each call. Entropy value was then transformed into relative entropy value (the entropy divided by the logarithm of the number of clusters) (Peet, 1974; Pielou, 1969). We then calculated the mean of these relative entropy values. This computation was performed for a number of clusters varying from 2 to 6 (optimal number of clusters range).

It should be noted that Fischer and colleagues (2017) have also proposed a procedure to quantify the degree of gradation in a vocal repertoire from a fuzzy clustering algorithm (Wadewitz et al. 2015; Fischer et al. 2017b). They used 'typicality coefficients' (Wadewitz et al. 2015) that describe the proportion between typical calls (calls having a high probability to

belong to a cluster) and atypical calls (calls having a low probability to belong to a cluster), and allow to conclude on the homogeneity of each cluster. However, our objective was to calculate an overall degree of gradation, without threshold, in a comparative approach. This is why we chose a measure based on the entropy value, which allows to estimate the overall degree of gradation of a repertoire according to the logic of information theory.

2.5.5. Statistical comparisons

We compared the optimal number of clusters between species with a generalised linear model using a Poisson family (GLM). We compared the relative entropy value (i.e. the degree of gradation between clusters) using linear models (LM). We compared the full models (i.e. with species as predictor factor) to the null models (i.e. without species) by applying likelihood ratio tests (LRT) using the function *lrtest* of the package *lmtest* (Zeileis and Hothorn 2002). This allowed to assess whether the species factor had a significant effect. When species had a significant effect, we performed post-hoc tests to make pairwise comparisons using the function *emmeans* of the package *emmeans* (Lenth et al. 2018).

3. Results

3.1.Acoustic distance

In the agonistic context, pairwise comparisons in the multivariate acoustic distances yielded significant differences between species, except between Japanese and Tonkean macaques; the distances between rhesus and Tonkean macaques remained limited relative to other distances between species (Fig. 1 & Supplementary material S1, Table 1). In the affiliative context, comparisons also yielded significant differences, except between Japanese and rhesus macaques; the distances between Tonkean macaques and either Japanese or rhesus macaques were limited (Fig. 1 & S1, Table 1). In the neutral context, all pairwise comparisons produced significant differences, but distances between Japanese, rhesus and Tonkean macaques were limited; crested macaques were farther from the other species in the three contexts (Fig. 1 & S1, Table 1). As an outcome, no grouping appeared between the Tonkean and crested macaques on one side, and Japanese and rhesus macaques on the other side.

3.2. Vocal diversity

In the agonistic context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 28.1$, $p < 0.001$), meaning that they differed in their number of groups of calls. Post-hoc tests revealed that the Tonkean/crested pair had a significantly greater number of clusters than the Japanese/rhesus pair; no significant differences were found between the two

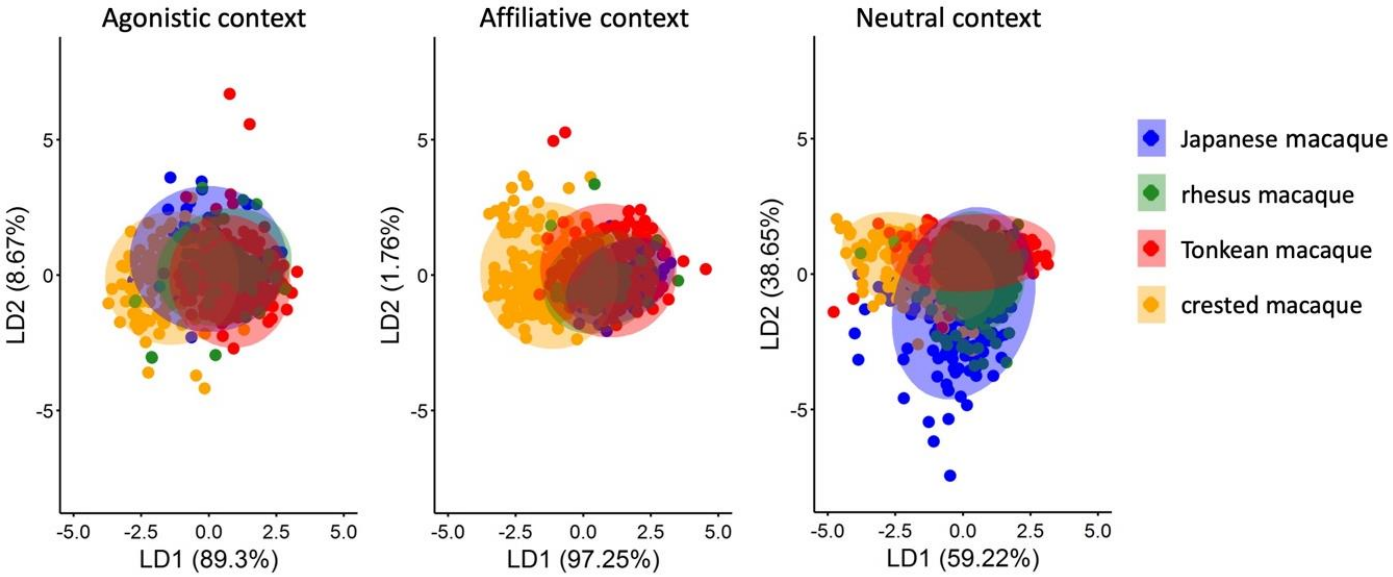


Fig. 1. Comparisons of acoustic distances between species for calls emitted in the agonistic, affiliative and neutral contexts: Linear Discriminant Analysis biplot with the four groups centroids of species on the first two linear discriminants (LD1 & LD2). The ellipses correspond to the 95% confidence interval.

members of each pair (Tonkean/crested macaques pair; Japanese/rhesus pair) (Fig. 2 & S1, Table 2). In the affiliative context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 90.4$, $p < 0.001$). Post-hoc tests showed that the Japanese macaques had a significantly smaller number of clusters than the other species; rhesus macaques had a lower number of clusters than the Tonkean/crested pair although the difference was significant with the crested macaques and not with the Tonkean macaques; Tonkean and crested macaques did not differ in their numbers of clusters (Fig. 2 & S1, Table 2). In the neutral context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 88.3$, $p < 0.001$). Post-hoc tests revealed that rhesus macaques had a significantly greater number of clusters than the other species); Tonkean macaques had a similar number of clusters compared to crested macaques; Japanese macaques had a significantly smaller number of clusters than the other species (Fig. 2 & S1, Table 2).

We used the truncation of the mean optimal number (*N*) of clusters for each species and context to illustrate the optimal grouping of call types usually recognized in macaque species (see Supplementary materials S1, Table 3, and S2, 3D cluster graphs). Although call types such as screams, barks, and coos were common to the four species, other types of calls were specific

to species: girneys and growls in Japanese and rhesus macaques, and soft grunts, hard grunts and chuckles in Tonkean and crested macaques (S1, Table 3).

3.3. Vocal flexibility

In the agonistic context, the mean relative entropy value was significantly different between species (LRT $\chi^2 = 1092$, $p < 0.001$), meaning that they varied in the degree of gradation between call types. Post-hoc tests showed that the strongest differences opposed the Japanese/rhesus pair to the Tonkean/crested pair, with the latter displaying higher entropies than the former; additionally, Tonkean macaques had a higher relative entropy than crested macaques, and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2 & S1, Table 2). In the affiliative context, the relative entropy value was significantly different between species (LRT $\chi^2 = 679$, $p < 0.001$). Post-hoc tests revealed that the strongest differences opposed the Japanese/rhesus pair to the Tonkean/crested pair, with the Tonkean/crested pair displaying a higher entropy than the Japanese/rhesus pair; crested macaques had a higher entropy than Tonkean macaques, and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2 & S1, Table 2). In the neutral context, the relative entropy value was significantly different between species (LRT $\chi^2 = 737$, $p < 0.001$). Post-hoc tests revealed no clear pattern contrasting the Japanese/rhesus to the Tonkean/crested pairs; rhesus macaques had a higher entropy compared to the other species; Japanese macaques had a higher relative entropy compared to Tonkean and crested macaques, and crested macaques had a higher entropy than Tonkean macaques (Fig. 2 & S1, Table 2).

4. Discussion

We found that the vocalisations of the four species of macaques studied differed in several respects. Although call types such as screams, barks, and coos were common to all of them, other types of calls were specific to species, consistently with the results of previous studies: girneys and growls in Japanese and rhesus macaques, and soft grunts, hard grunts and chuckles in Tonkean and crested macaques (Green, 1975; Masataka & Thierry, 1993; Rowell & Hinde, 1961; Peters, 1983; Panggur, 2013). The analysis of the acoustic distances between the sets of calls recorded in each species for each context confirmed that each macaque species has its own acoustic repertoire (see Gouzoules et al. 2000). In particular, we did not find any significant contrasts in acoustic distances that would allow to arrange the sets of calls of Japanese macaques and rhesus on one side, and Tonkean and crested macaques on the other side.

We addressed vocal diversity by identifying the optimal number of groups of calls in each species. This showed that the Japanese/rhesus pair differed from the Tonkean/crested pair in the agonistic context; the latter had one additional group of calls compared to the former. It

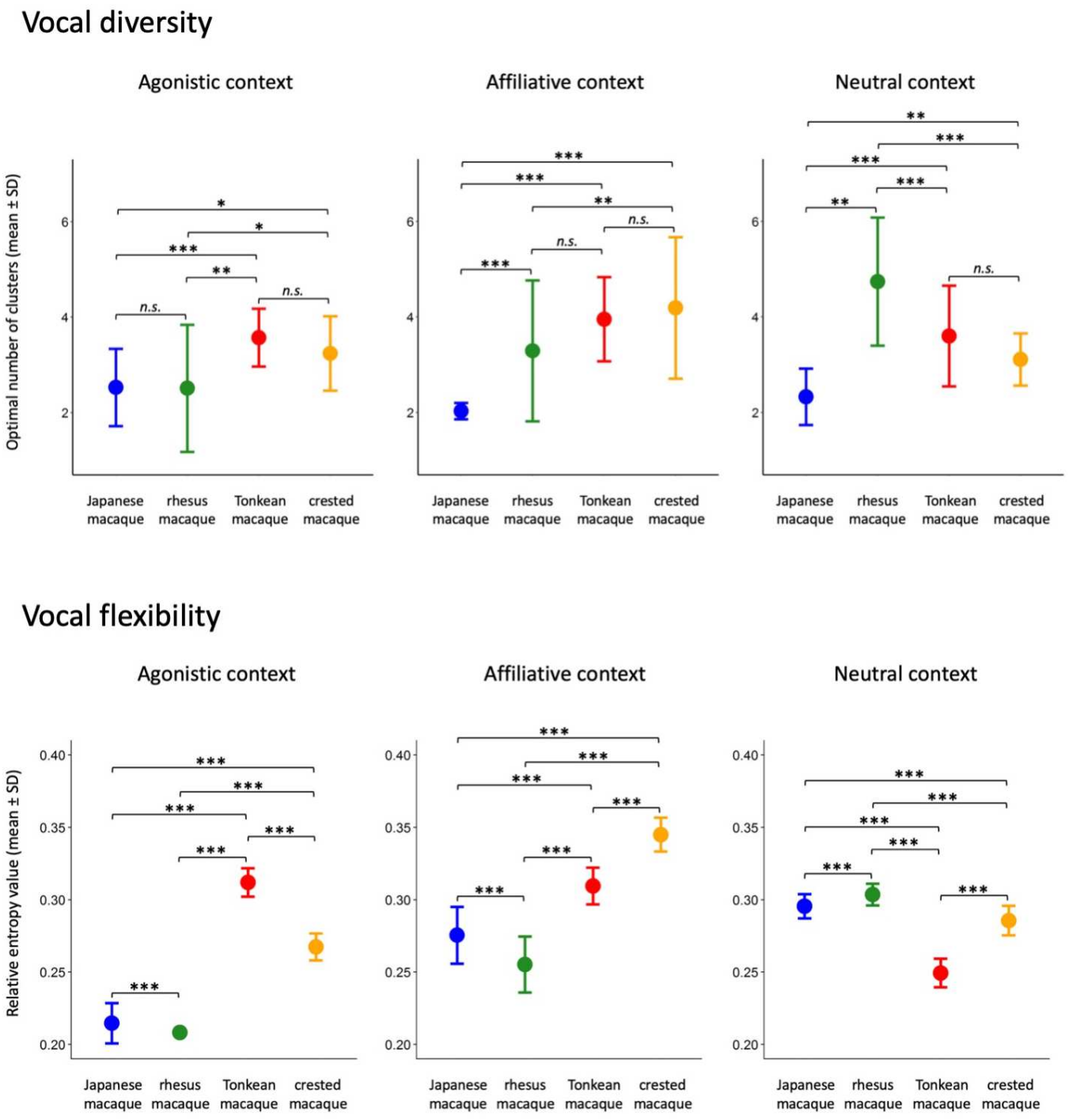


Fig. 2. Comparisons of vocal diversity and flexibility between species for calls emitted in the agonistic, affiliative and neutral contexts: optimal numbers of clusters and entropy values (* < 0.001, **p < 0.01, *p < 0.05).**

Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

Based on the interspecies contrasts evidenced in the acoustic structure of calls, we can reject the null hypothesis that there should be no difference between the Tonkean/crested and Japanese/rhesus pairs. With regard to the phylogenetic hypothesis, it posits that closely related species should show generalised similarity in calls for any acoustic variable and social context. This fails to explain why the two pairs of species differed in the number of groups of calls and the degree of gradation between them, but not in their acoustic distances, nor why the contrasts were consistent in the agonistic context, but not in the other social contexts. By contrast, the social complexity hypothesis is able to account for these various results. It predicts that only complexity variables – vocal diversity measured by the number of groups of calls and vocal flexibility measured by the degree of gradation – should differ between the Tonkean/crested and Japanese/rhesus pairs in the agonistic context. It also expects that the magnitude of contrasts between the two pairs of species should be less pronounced or absent in the affiliative and the neutral context.

The contrasts encountered between species in the neutral context did not follow any pattern related to variations in the degree of social uncertainty between pairs of species. As callers did not receive specific responses from their groupmates in the neutral context, the stakes are not very high in terms of social risks, it is understandable that vocal complexity was not influenced by the species-specific style of social interactions. With regard to affiliative interactions, no more patterns were uncovered regarding vocal diversity, but we found that Tonkean/crested pair displayed a higher degree of gradation in their calls than the Japanese/rhesus pair. It could be that calls occurring in affiliative interactions incur more consequences than calls emitted in the neutral context (see Blount 1985; Katsu et al. 2017) – although less than those produced in the context of aggression – which would explain that vocal flexibility can be affected by the degree of uncertainty of the social interactions.

The social interactions of tolerant macaque species are characterized by a higher degree of freedom than those of more intolerant macaques, as they are less constrained by kinship and dominance relations (Thierry, 1990; Butovskaya, 2004; Flack & de Waal, 2004; Duboscq et al., 2017). Functionally, a greater diversity of vocal signals and a marked gradation between them can provide richer and more nuanced meanings, as moving gradually from one display to another would allow the signals to express a broad motivational spectrum (Morton, 1977; Freeberg et al., 2012). In other words, such signals have the potential to contain a large amount of information and convey a wide range of emotions and intentions. This would contribute to the developed negotiation skills of tolerant macaques, enabling them to manage undecided open contests and achieve high rates of conflict resolution (de Waal 1993; Petit & Thierry 1994; Thierry 2007; De Marco et al. 2014; Duboscq et al. 2014). If this is true as expected in the agonistic context, it may also apply to the affiliative context where a greater richness of

communication signals could help individuals choose the best solution from a variety of behavioural options.

It should be stressed that our results are by nature correlational. The causal direction of the social complexity hypothesis for communicative complexity is still debated (Peckre et al. 2019). While complex social situations may require complex communicative abilities, complex communicative abilities may also foster the emergence of complex social interactions. Since the two processes are not mutually exclusive, a positive feedback loop may occur between them at the evolutionary level. In addition, it is generally assumed that the social complexity hypothesis applies to entire social systems. Our results reveal that the hypothesis can hold for some social situations and not for others. In particular, we did not find consistent differences between tolerant and intolerant macaques in the neutral context, where most of the recorded calls were coos and growls. As mentioned above, it is consistent that no link between social and communicative complexity has emerged in a context where callers were not involved in social interactions.

We have studied the calls of three species of macaque in captive settings, and in nature for the fourth, but we found no contrast between groups that could be attributed to the recording conditions. Furthermore, while Japanese, Tonkean and crested macaques are mainly forest-dwelling species, rhesus macaques can live in quite diverse habitats. Again, our analyses did not reveal systematic contrasts between rhesus macaques and the other three species. It is known that the physical structure of the habitat can affect the frequency or amplitude of auditory signals for example (Waser & Brown 1986; Hauser 1996), but we have relied on variables related to vocal diversity and flexibility, for which no influence of ecological conditions is assumed to date (Freeberg et al. 2012). Future research should confirm the contrasts in vocal diversity and flexibility found between tolerant and intolerant macaques by extending the analyses to a larger number of groups and species. The additional study of the combinations of calls in vocal sequences and the responses of listeners (Kershenbaum et al. 2014) will also be necessary to test the social complexity hypothesis in a comprehensive way.

Supplementary material S1

from "Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication"

Table 1. Acoustic distances: results of linear discriminant analyses for pairwise distances between species in each social context.

Pairwise comparisons	Agonistic context		Affiliative context		Neutral context	
	distance	*p*	distance	*p*	distance	*p*
Japanese vs. rhesus macaque	718	0.001	85.7	0.077	211	< 0.001
Japanese vs. Tonkean macaque	206	0.167	247	< 0.001	106	0.025
Japanese vs. crested macaque	1006	< 0.001	669	< 0.001	565	< 0.001
rhesus vs. Tonkean macaque	513	< 0.001	161	0.033	105	< 0.001
rhesus vs. crested macaque	1727	< 0.001	584	< 0.001	776	< 0.001
Tonkean vs. crested macaque	1211	< 0.001	422	< 0.001	670	< 0.001

Table 2. Vocal diversity and flexibility: results of post-hoc pairwise comparisons between species in each social context.

Pairwise comparisons	Agonistic context				Affiliative context				Neutral context			
	estimate	*SE*	*t*	*p*	estimate	*SE*	*t*	*p*	estimate	*SE*	*t*	*p*
Vocal diversity: mean optimal number of clusters												
Japanese vs. rhesus macaque	+ 0.008	0.089	+ 0.09	0.999	- 0.483	0.089	- 5.41	< 0.001	- 0.710	0.080	- 8.88	< 0.001
Japanese vs. Tonkean macaque	- 0.344	0.082	- 4.19	< 0.001	- 0.666	0.086	- 7.71	< 0.001	- 0.435	0.084	- 5.17	< 0.001
Japanese vs. crested macaque	- 0.247	0.084	- 2.95	0.017	- 0.725	0.086	- 8.47	< 0.001	- 0.289	0.087	- 3.33	0.005
rhesus vs. Tonkean macaque	- 0.352	0.082	- 4.28	< 0.001	- 0.183	0.075	- 2.45	0.068	+ 0.275	0.070	+ 3.94	< 0.001
rhesus vs. crested macaque	- 0.255	0.084	- 3.04	0.013	- 0.242	0.074	- 3.28	0.006	+ 0.421	0.073	+ 5.78	< 0.001
Tonkean vs. crested macaque	+ 0.097	0.077	+ 1.26	0.586	- 0.059	0.070	- 0.84	0.835	+ 0.146	0.077	+ 1.89	0.232
Vocal flexibility: mean entropy value												
Japanese vs. rhesus macaque	+ 0.006	0.002	+ 4.02	< 0.001	+ 0.020	0.002	+ 8.78	< 0.001	- 0.008	0.001	- 6.30	< 0.001
Japanese vs. Tonkean macaque	- 0.097	0.002	- 61.4	< 0.001	- 0.034	0.002	- 14.8	< 0.001	+ 0.046	0.001	+ 36.1	< 0.001
Japanese vs. crested macaque	- 0.053	0.002	- 33.2	< 0.001	- 0.070	0.002	- 30.2	< 0.001	+ 0.010	0.001	+ 7.73	< 0.001
rhesus vs. Tonkean macaque	- 0.104	0.002	- 65.4	< 0.001	- 0.054	0.002	- 23.6	< 0.001	+ 0.054	0.001	+ 42.4	< 0.001
rhesus vs. crested macaque	- 0.059	0.002	- 37.3	< 0.001	- 0.090	0.002	- 39.0	< 0.001	+ 0.018	0.001	+ 14.0	< 0.001
Tonkean vs. crested macaque	+ 0.045	0.002	+ 28.2	< 0.001	- 0.036	0.002	- 15.4	< 0.001	- 0.036	0.001	- 28.4	< 0.001

Table 3. Distribution of call types per cluster for each species and social context.

Context and species	Cluster No[1]	Bark	Hard grunt	Scream	Screech	Rattle	Gecker	Chuckle	Growl	Girney	Soft grunt	Affiliat-ive call	Coo	Food call	Unclass-ified[2]
Agonistic context															
Japanese macaque	1	7	0	25	0	2	0	3	3	0	0	0	3	2	8
Japanese macaque	2	0	0	17	0	1	0	0	0	0	0	0	0	1	7
rhesus macaque	1	58	0	5	0	0	1	0	18	0	0	0	0	0	0
rhesus macaque	2	8	0	19	0	0	1	4	0	0	0	0	0	0	4
Tonkean macaque	1	1	8	9	3	1	3	9	0	0	2	0	1	0	14
Tonkean macaque	2	2	4	1	0	22	9	28	0	0	4	0	5	0	19
Tonkean macaque	3	5	12	7	11	13	3	29	0	0	5	0	10	0	30
crested macaque	1	0	5	1	0	5	4	42	0	0	0	0	1	0	13
crested macaque	2	3	8	38	0	2	0	13	0	0	1	0	2	0	13
crested macaque	3	0	2	38	0	1	0	4	0	0	0	0	0	0	5
Affiliative context															
Japanese macaque	1	0	0	0	0	0	0	0	10	15	1	0	29	0	4
Japanese macaque	2	0	0	0	0	0	0	0	2	4	0	0	26	2	1
rhesus macaque	1	0	0	0	0	0	0	0	2	1	0	0	0	0	1
rhesus macaque	2	0	0	0	0	0	0	0	1	0	0	0	0	3	0
rhesus macaque	3	0	0	0	0	0	0	0	40	5	0	3	1	0	2
Tonkean macaque	1	0	4	0	0	1	0	0	0	0	84	5	39	0	5
Tonkean macaque	2	0	2	2	0	0	0	0	0	2	14	0	2	0	0
Tonkean macaque	3	0	0	0	0	0	0	0	0	0	28	0	36	0	2
crested macaque	1	0	0	0	0	0	0	0	0	4	15	0	22	0	5
crested macaque	2	0	0	0	0	0	0	8	0	0	15	0	13	0	2
crested macaque	3	0	0	0	0	0	0	0	0	5	32	2	37	0	15
crested macaque	4	0	0	0	0	0	0	4	0	0	58	3	37	0	20
Neutral context															
Japanese macaque	1	0	0	0	0	0	0	0	0	6	0	0	121	73	0
Japanese macaque	2	0	0	6	0	0	0	0	0	0	0	0	15	34	0
rhesus macaque	1	7	0	0	0	0	0	0	130	0	0	10	6	0	2
rhesus macaque	2	9	0	1	0	0	0	0	12	0	0	0	31	38	1
rhesus macaque	3	0	0	0	0	0	0	0	0	0	0	0	35	5	0
rhesus macaque	4	25	0	0	0	0	1	0	52	0	0	0	51	41	4
Tonkean macaque	1	0	0	0	1	0	0	1	0	0	21	0	67	0	3
Tonkean macaque	2	0	0	2	0	1	0	9	0	0	9	0	1	0	2
Tonkean macaque	3	0	0	0	0	0	0	0	0	0	2	0	81	2	0
crested macaque	1	2	1	0	0	0	0	2	0	0	0	0	43	0	8
crested macaque	2	1	7	0	0	0	0	11	0	0	0	0	84	0	18
crested macaque	3	0	1	0	0	0	0	0	0	0	0	0	13	0	0

[1]Numbers correspond to the *n* different clusters identified by the clustering method.

[2]Calls that could not be assigned to recognized call types.

References on the call types recognized in macaques

Green S (1975) Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In: LA Rosenblum (ed), Primate behavior: developments in field and laboratory research, Vol 4. Academic Press, New York, NY, pp 1–102

Lewis SA (1985) The vocal repertoire of the Celebes black ape (*Macaca nigra*). PhD thesis, University of Georgia, Athens, GA

Lindburg DG (1971) The rhesus monkey in North India: an ecological and behavioral study. In LA Rosenblum (ed), *Primate behavior: developments in field* and laboratory research, Vol 2. Academic Press, New York, NY, pp 1–106

Masataka N, Thierry B (1993) Vocal communication of Tonkean macaques in confined environments. Primates 34:169–182

Panggur MR (2013) Vocal communication of wild crested macaques (*Macaca nigra)*. MS thesis, Bogor Agriculture, Bogor University.

Peters EH (1983) Vocal communication in an introduced colony of feral rhesus monkeys (*Macaca mulatta*). PhD thesis, University of Florida, Gainesville, FL

Rowell TE, Hinde RA (1962) Vocal communication by the rhesus monkey (*Macaca mulatta*). Proc Zool Soc Lond 138, 279–294.

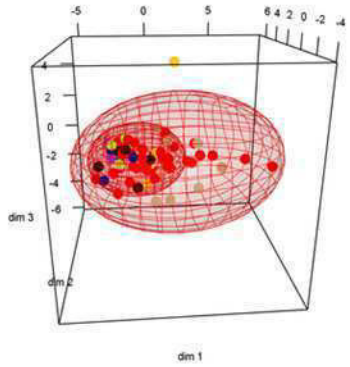
Supplementary material S2

from "The structure of vocal signals in four species of macaque: a comparative test of the social complexity hypothesis"

3D CLUSTER GRAPHS

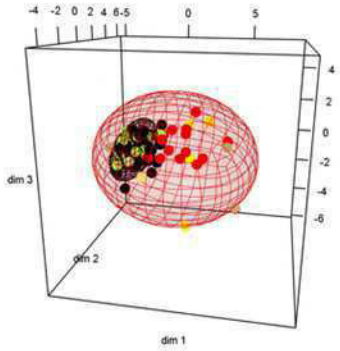
Dispersion of data for the first three dimensions of the PCAs in each species of macaque and social context: agonistic context (slide 2), affiliative context (slide 3) and neutral context (slide 4). The clusters are shown with 95% confidence ellipses around cluster centroids. The axes correspond to the PCA axes

Using the animation function of Powerpoint, it can be seen on the rotating graphs at which cluster each dot belongs. This shows that the composition of clusters differs according to the species. The larger the space occupied by the cluster in the common acoustic space, the greater the variability of the calls. For calls of rhesus macaques emitted in the affiliative context, for example, the small size of the clusters reflects the low degree of variability of their growl.

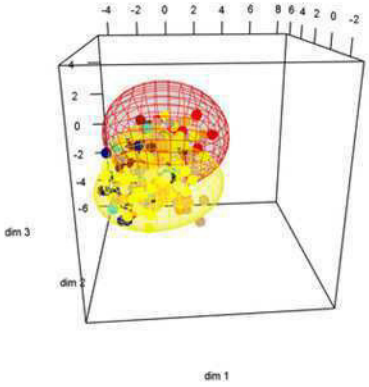


Agonistic context

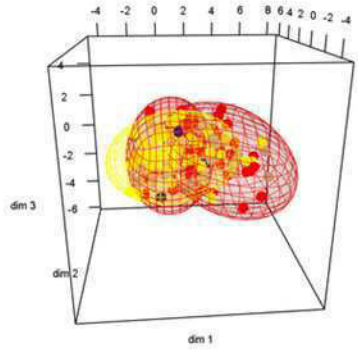
Japanese macaque



rhesus macaque



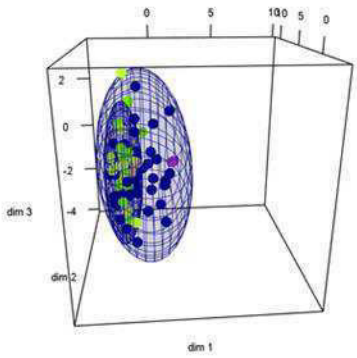
Tonkean macaque



crested macaque

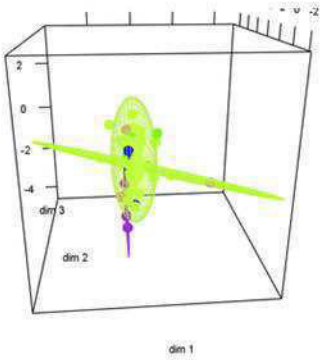
Call types

- bark
- hard grunt
- scream
- screech
- rattle
- gecker
- chuckle
- growl
- soft grunt
- coo
- unidentified



Affiliative context

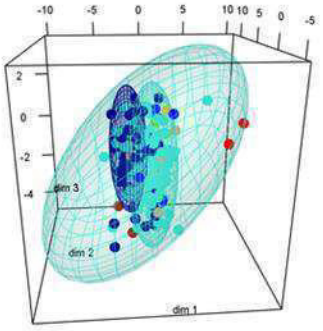
Japanese macaque



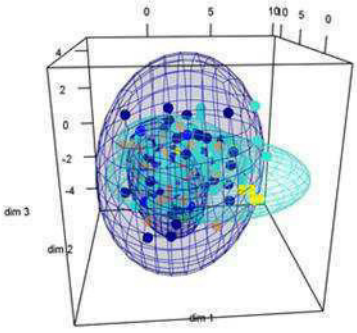
rhesus macaque

Call types

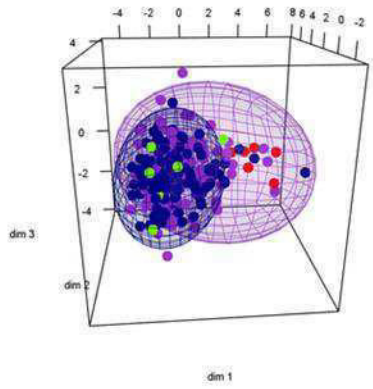
- scream
- chuckle
- growl
- girney
- soft grunt
- affiliative call
- coo
- food call
- unidentified



Tonkean macaque

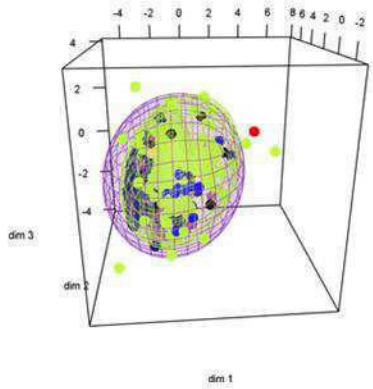


crested macaque



Neutral context

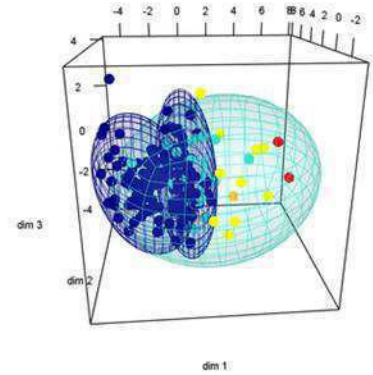
Japanese macaque



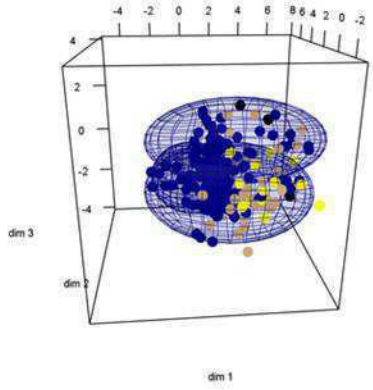
rhesus macaque

Call types

- bark
- hard grunt
- scream
- screech
- rattle
- gecker
- chuckle
- growl
- soft grunt
- affiliative call
- coo
- food call
- unidentified

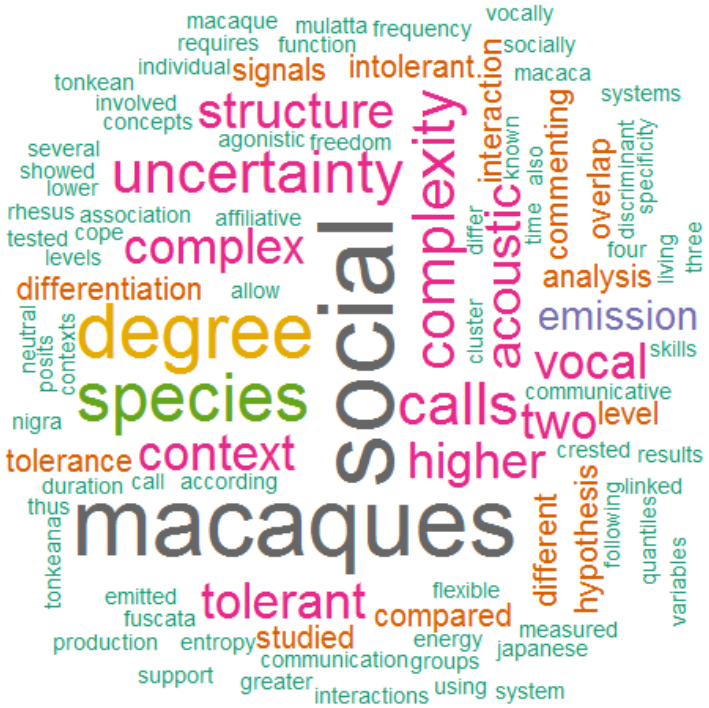


Tonkean macaque



crested macaque

CHAPTER 6
Tolerant and intolerant macaques differ in the context specificity of their vocal signals



Abstract

The social complexity hypothesis for communicative complexity posits that living in a complex social system requires complex communication skills. Since the complexity of a system can be measured by the amount of uncertainty it can produce, we could test this hypothesis by studying several species of macaque that differ by their level of social tolerance and the degree of uncertainty of their social interactions. We studied vocal communication in several groups of macaque belonging to four species: Japanese and rhesus macaques, which are characterized by low levels of social tolerance and whose outcome of interactions is highly predictable; and Tonkean and crested macaques, which display high levels of social tolerance and uncertainty in their social interactions. We recorded the vocalizations emitted by adult females in three social contexts: affiliative, agonistic, and neutral. We measured call duration, entropy, and time and frequency energy quantiles, and processed these variables using cluster and discriminant function analyses. We found that tolerant macaques have a lower degree of overlap than intolerant ones between the acoustic structure of calls and their context of emission; the use of signals that are weakly dependent on context can offer the former with a wider range of expression. The study of commenting calls made by individuals attending social interaction between groupmates also showed that their acoustic structure was more differentiated from other calls in tolerant than in intolerant macaques; this should allow commenting individuals to get out of their own situation and spread information about ongoing events. The flexibility of vocal production therefore appears to be correlated with the level of uncertainty of social interactions. Species with more complex social interactions were also those with higher degree of freedom in the association between acoustic structure and social context, which supports the social complexity hypothesis.

Keywords

Social complexity, uncertainty, flexibility, communication, acoustics, non-human primates

Manuscript to be submitted soon

Tolerant and intolerant macaques differ in the context specificity of their vocal signals

1. Introduction

Living in a complex social system means interacting with different social partners in a variety of situations. This social complexity, in turn, requires sophisticated communicative skills so that individuals can express a wide range of intentions and emotional states. This is what posits the *social complexity hypothesis for communicative complexity*, which has become a topical issue in recent years (Pollard and Blumstein 2012; Freeberg et al. 2012a; Peckre et al. 2019). When testing this hypothesis, however, a recurring problem is the definition and measure of complexity (Bergman and Beehner 2015; Peckre et al. 2019; Chapter 3). The preferred measures of social complexity are the number of individuals in a social group (Freeberg 2006a; Lehmann and Dunbar 2009; Dunbar 2012; Bergman and Beehner 2015) and the different types of group members (Blumstein and Armitage 1997; Pollard and Blumstein 2012). However, these measures are rather crude proxies that do not consider how individuals interact (Shultz and Dunbar 2006). It has therefore been proposed to use the number of social interactions (Freeberg et al. 2012a) or the number of social relationships (Bergman and Beehner 2015; Fischer et al. 2017a). Such indices are valuable because they reflect social diversity, but diversity alone cannot yet sum up the entire complexity of social systems (Chapter 3).

With regard to vocal complexity, the variable most often considered is the number of units in a communicative system, and in particular the number of vocalizations in a species' repertoire (Pollard and Blumstein 2012; Freeberg et al. 2012a; Peckre et al. 2019). Another measure is the amount of information in a vocal repertoire, calculated as the number of bits of information using Shannon's entropy formula (Shannon 1948; Freeberg 2006; Bouchet et al. 2013). These two variables only concern vocal diversity. In addition, they are difficult to implement in animals with a graded repertoire, that is, a continuum of acoustic structures without clear boundaries between different types of calls (Hammerschmidt and Fischer 1998; Wadewitz et al. 2015). For this reason, it has been recommended to assess vocal complexity by quantifying the degree of gradation of the vocal repertoire (Wadewitz et al. 2015; Fischer et al. 2017b), and thus the flexibility of acoustic structures in a species (Chapter 5). It should be added that flexibility can also manifest itself in the extent of context specificity of vocal signals, i.e. the degree of freedom between their acoustic structure and the context in which they are emitted (Wheeler and Fischer 2012).

In animal communication, the relationship between structure and function is not a simple one. Many vocal signals are not context-specific and acoustically similar calls can occur in

different social situations, while acoustically dissimilar calls can be produced in the same social situations; this has led to the idea the acoustic structure of signals bears no particular relationship to their social function (see Owren & Rendall 2001). On the other hand, the motivation-structural rules proposed by Morton (1977) assume that there is a relationship between the physical structures of sounds and the motivation underlying them. Some sounds may be more likely than others to induce attention, arousal or emotional responses in conspecifics, and call structure may then be partially predicted from the context. In mammals, for example, affiliative contexts tend to be associated with higher amplitude, lower frequency modulation and less noisy signals than agonistic and alarm-related contexts (Morton 1977; Owren and Rendall 2001; Briefer 2012; Gustison and Townsend 2015). Flexibility in the degree of connection between vocal signals and their context of occurrence contributes to the complexity of communication systems (Manser et al. 2014; Pika 2017; Peckre et al. 2019).

Although there is no consensus on a general definition of complexity, there is agreement that the behaviour of complex systems is difficult to predict (McDaniel and Driebe 2005; Schuster 2016). It is, therefore, possible to assess the complexity of systems according to their ability to produce uncertainty (Chapter 3). When studying communicative complexity, we can rely on the degrees of freedom in the association between signals and their context of emission to tackle uncertainty. For example, a strong connection between a vocal signal and a given context implies a low degree of uncertainty in the system: when hearing a context-specific call, the listener does not need information about the context to identify the information encoded into the acoustic structure of the call; by contrast, when a call is little context-specific, uncertainty about the message is greater and the listener needs additional contextual cues to respond appropriately (Seyfarth & Cheney 2003; Wheeler and Fischer 2012; Manser et al. 2014).

While the strength of the association between the structure of a vocal signal and the context in which the caller is involved is variable, there is a further degree of freedom when calls are triggered by a context in which callers are not themselves involved. Such a situation has been reported in Barbary macaques (*Macaca sylvanus*) where a bystander may vocalize while attending an interaction between group mates (Brumm et al. 2005). The bystander is not involved in the social interaction and shows no other response than to vocalize, which is why Brumm and colleagues (2005) described these calls as ‘comments’. They suggest that the comments draw the attention of others to the event, but that they could also include an evaluation of the event (Brumm et al. 2005). It is not known whether commenting calls have a specific acoustic structure. If they were to differ from both calls emitted by individuals involved in social interaction and contact calls emitted in the absence of any interaction, such flexibility would make the communication systems more complex by providing individuals with a greater number of expressive options.

In an earlier study, we have found interspecific contrasts in the diversity and flexibility of the acoustic structure of vocal signals in four species of macaque. While phylogenetic relationships between species failed to account for these results, the social complexity hypothesis for communicative complexity successfully explained them (Chapter 5). Here we extend here the comparative study of flexibility by investigating the strength of the association between vocal structure and social context. Macaque species are well suited to these aims. All are semi-terrestrial primates living in multimale-multifemale groups, with males dispersing and females remaining in their natal group where they constitute matrilines, i.e. subgroups of relatives linked by maternal descent (Thierry 2007). Although they share the same basic patterns of organization, macaques show a wide range of variation regarding their degree of social tolerance, which is associated with varying levels of uncertainty in the outcome of agonistic interactions (Dobson, 2012; Zannella, Stanyon, & Palagi, 2017). In the most intolerant species, social conflicts have clear consequences: in Japanese macaques (*Macaca fuscata*) and rhesus macaques (*M. mulatta*), for example, the recipient of aggression flees or submits in nine out of ten cases among unrelated females (Thierry et al. 2008). By contrast, in more tolerant species the recipient of the aggression frequently protests or initiates a counter-attack: in Tonkean macaques (*M. tonkeana*) and crested macaques (*M. nigra*), 68.0% and 45.4% of conflicts among unrelated females, respectively, remain undecided, without clear winners or losers (Thierry et al. 2008). The interspecific variations reported in the agonistic patterns of macaques co-vary with other components of their social style. Tolerant macaques reconcile more often and have a greater number of facial displays than their more intolerant counterparts, they perform better in experimental tasks requiring individuals to display inhibitory control or pointing gestures, and their social behaviours are less constrained by kinship and dominance relationships than those of the latter (Thierry 2007; Dobson 2012; Balasubramaniam et al. 2017; Joly et al. 2017).

In this study, we compare two tolerant species (Tonkean & crested macaques) and two intolerant species (Japanese & rhesus macaques). They are mainly frugivorous primates, their primary habitat is forest, with the exception of rhesus macaques which can live in diverse habitats, from forests to arid lands or regions of human settlement (Ménard 2004). They use a graded repertoire of vocalizations (Rowell and Hinde 1962; Green 1975a; Masataka and Thierry 1993; Gouzoules and Gouzoules 2000; Panggur 2014). From the social complexity hypothesis for communicative complexity, it can be predicted that the degree of flexibility of a communicative system is related to the degree of uncertainty of social interactions and relationships. On the basis of this reasoning, we will examine the structure of the vocal signals produced in three different social contexts (agonistic, affiliative, neutral) to test the following two predictions: (1) *Overlap between structure and context*: analysis of the acoustic structure of calls according to the contexts in which callers are placed should reveal that the degree of

overlap of acoustic structures with contexts is more pronounced in tolerant than in intolerant macaques; (2) *Differentiation of commenting calls*: analysis of the acoustic structure of comments made by bystanders should reveal that their degree of differentiation from other categories of calls – i.e. calls emitted by individuals involved in social interactions, or contact calls emitted in the absence of any interaction – is more pronounced in tolerant than in intolerant macaques.

2. Methods

2.1. Subjects and living conditions

We conducted behavioural observations and acoustic recordings of 29 adult females from two groups of Japanese macaques, 16 adult females from two groups of rhesus macaques, 13 adult females from four groups of Tonkean macaques, and 51 adult females from two groups of crested macaques. We focused on adult females because they are the most represented age-and-sex category in macaque social groups, and also the most active contributors in vocal communication (Lemasson et al. 2013a). Japanese, rhesus and Tonkean macaque females were captive-born and at least five years old. Crested macaques were studied in nature, and the age of the subjects was assessed according to their reproductive history since 2006 (Macaca Nigra Project, www.macaca-nigra.org), their body size, the shape of their nipples, and the presence of old physical injuries. The composition of groups is given in Table 1.

The groups of Japanese macaques (Ft, Fw) were housed in two enclosures of 960 and 4,600 m², respectively, at the Primate Research Institute in Inuyama, Japan (Arlet et al. 2015). The groups of rhesus macaques (Ma, Mb) were housed in two 210-m² enclosures at the Biomedical Primate Research Center in Rijswijk, The Netherlands (De Marco et al. 2019). One group of Tonkean macaques (Tb) was housed at the Orangerie Zoo in Strasbourg, France, in a 120-m² enclosure, and the other three groups (Tc, Td, Te) were housed at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy, in 500-m² enclosures (De Marco et al. 2019). Enclosures were wooded or furnished with perches, ropes, and shelters. Animals were fed commercial monkey diet pellets, supplemented with fresh fruits and vegetables, and water was available ad libitum. The groups of crested macaques (Npb, Nr1) lived in the Tangkoko Nature Reserve, North Sulawesi, Indonesia (Micheletta et al. 2015). They were not provisioned and inhabit lowland tropical rainforest (Collins et al. 1991; Rosenbaum et al. 1998).

The study complied with the legal requirements and guidelines of the Japanese, Dutch, Italian, and French governments, and followed the ASAB/ABS guidelines for the treatment of animals in behavioural research.

Table 1. Information about groups and subjects (Takahashi et al. 2006; Micheletta et al. 2013; Arlet et al. 2015; De Marco et al. 2019).

Groups	Dates of group foundation and study	Composition of groups	Name and age in years of females[1]
rhesus macaque group Ma	founded in 2004, studied in Jul–Oct 2016	10 adult females, 3 adult males, 22 immatures[2]	*Pip* (14), *But* (13), *Isa* (11), *Nil* (10), *Hoe* (10), *Wie* (9), *Lok* (7), *Aus* (6), *Mon* (5), *Pan* (5)
rhesus macaque group Mb	founded in 2004, studied in Jul–Oct 2016	6 adult females, 1 adult male, 24 immatures	*Tro* (13), *Plo* (12), *Hat* (10), *Jah* (8), *Kwe* (7), *Ymi* (6)
Tonkean macaque group Tb	founded in 1978, studied in Feb–May 2016	4 adult females, 6 adult males, 5 immatures	*Gil* (27), *Gai* (9), *Giu* (9), *Lis* (5)
Tonkean macaque group Tc	founded in 2005, studied in Sept–Dec 2014	4 adult females, 4 adult males, 8 immatures	*Pal* (13), *Sop* (11), *Pam* (8), *Pap* (6)
Tonkean macaque group Td	founded in 2007, studied in Mar–May 2015	3 adult females, 5 adult males, 7 immatures	*Sib* (12), *Tet* (11), *Tan* (11)
Tonkean macaque group Te	founded in 2009, studied in Sept–Dec 2014	2 adult females, 3 adult males, 5 immatures	*Nin* (15), *Nif* (9)
Japanese macaque group Fw	founded in 1974, studied in Mar–Aug 2005	13 adult females, 4 adult males, 10 immatures	*Has* (10), *Min* (6), *Mia* (5), *Nir* (6), *Rek* (14), *Rum* (17), *Mil* (9), *Bel* (5), *Lar* (5), *Som* (18), *Sar* (8), *Jes* (7), *Ren* (20)
Japanese macaque group Ft	founded in 1970/1971, studied in Mar–Jul 2005	16 adult females, 6 adult males, 24 immatures	*Ame* (25), *Iwa* (11), *Kak* (8), Kin (15), Kam (5), Kur (9), *Mor* (22), Shi (10), Sha (8), *Tan* (24), *Tak* (17), *Tsu* (21), *Umi* (19), *Ume* (8), *Yam* (13), *Yuk* (21)
Crested macaque group Nr1	wild population, studied between Sept 2010 & Apr 2011	28 identifiable adult females,10 adult males, 42 immatures	*Ani*, Adi, Bea, Bas, *Cin*, Dor, Ern, Fen, *Glo*, *Hel*, Isa, *Jos*, Kat, *Leo*, *Min*, *Nur*, Oli, Pol, Qut, *Ros*, *Sup*, *Tut*, Eli, Vod, Wi, Big, Yan, Zoe
Crested macaque group Npb	wild population, studied between Sept 2010 & Apr 2011	23 identifiable adult females,8 adult males, 29 immatures	*Agn*, *Bia*, *Cic*, Dea, *Eva*, Fio, Geu, Her, Iye, Jan, *Kri*, Lid, Nao, Oma, *Ram*, *Ste*, *Jam*, Mal, Zor, Pap, Val, Tem, Upi

[1]Age at the beginning of data collection. The names of the sampled females are in italics.

[2]Individuals under 5 years of age.

2.2. Data collection

We carried out observations outdoors to ensure the quality of the recordings. Data were collected by A.L. in Japanese macaques (Arlet et al. 2015), N.R. in rhesus macaques, A.D.M., A.S., and N.R. in Tonkean macaques (De Marco et al. 2019), and J.M. in crested macaques (Micheletta et al. 2015) (Table 1). We observed subjects in a predefined random order using focal sampling. The sample duration was 10 mn in Japanese, crested macaques, and Tonkean macaques from groups Tc, Td and Te, and 15 mn in rhesus macaques and Tonkean macaques from group Tb. This resulted in 6.1 ± 0.16 h of focal sampling per female in Japanese macaques, 12.7 ± 0.7 h in rhesus macaques, 13.6 ± 3.2 h in Tonkean macaques, and 7.8 ± 0.4 in crested macaques.

For Japanese macaques, we recorded vocalizations with a TCD-D100 Sony (Tokyo, Japan) DAT recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and an ECM 672 Sony directional microphone. For rhesus and Tonkean macaques, we used a Marantz (Eindhoven, The Netherlands) PMD 661 recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits), and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. For crested macaques, we used partly a high-resolution camera Panasonic (Osaka, Japan) HDC-SD700 linked to a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. We extracted the audio tracks from the video recordings using the software *FFmpeg* (v 3.4.1) leading to WAV format audio files (sampling frequency: 32 000 Hz, resolution: 16 bits). We collected observational data about the context of call emission with a lavalier microphone connected to the recorder in Japanese, rhesus and Tonkean macaques (at805f, audio-technica, Leeds, United Kingdom vs TCM 160, Meditec, Singapore). In the crested macaques, the observer filmed the focal individual while a field assistant recorded contextual data using a handheld computer.

We distinguished three social contexts: agonistic, affiliative and neutral. They were defined according to the behaviours that could occur in the 3 s before or after the emission of a call or a sequence of calls. A sequence was itself defined as a series of calls separated by a maximum of 3 s. Behavioural units were based on published repertoires for macaques (Altmann 1962; Fedigan 1976; Thierry et al. 2000a). The agonistic context included aggression (supplantation, lunge, chase, slap, grab, bite, facial threat display) and response to aggression (aggression, avoidance, flight, crouch, submissive facial displays). The affiliative context included affiliative behaviours (approach, sitting in contact, social grooming, social play, grasp, embrace, mount, affiliative facial display). In the neutral context, the caller was not involved in a social interaction.

To investigate the degree of differentiation of commenting calls, we distinguished three categories of calls according to the degree of involvement of callers in social interactions: *Interaction call*: the caller is engaged in social interaction (i.e. agonistic or affiliative) in the 3 s before or after the utterance of a call or a sequence of calls. *Commenting call*: a social interaction occurs in the 3 s before the utterance of the call or the sequence of calls but the caller is not involved in the interaction. *Uncontextualized call*: no social interactions occur in the 3 s before or after the emission of a call or a sequence of calls; we have removed from the analysis the calls and sequences of calls where a non-social event (e.g. any event related to human activity) occurred in the 3 s preceding it. Note that all uncontextualized calls could be identified by the human ear as coos or growls. Also note that from the point of view of the signaler's calls, both commenting and uncontextualized calls occurred in the neutral context. We could not distinguish these two types of calls in Japanese macaques because the observer did not record social interactions other than those in which the caller was directly involved.

2.3. Acoustic analysis

We had recordings of 1368 calls in Japanese macaques, 1026 calls in rhesus macaques, 1210 calls in Tonkean macaques, and 1234 calls in crested macaques. We drew spectrograms using the software Raven Pro v1.4' (Cornell Lab of Ornithology, www.birds.cornell.edu/raven) with a 256 fast Fourier transform length and a Hanning window. With the same software, we measured the following variables: *Duration*: duration from the beginning to the end of a call, in seconds; *Q2 ratio*: ratio between duration that divides a call into two intervals of equal energy and duration, in percentage; *Q1 frequency*: value of the frequency that divides a call into two intervals containing 25% and 75% of the energy, in Hertz; *Q2 frequency*: value of the frequency that divides a call into two intervals of equal energy, in Hertz; *Q3 frequency*: value of the frequency that divides a call into two intervals containing 75% and 25% of the energy, in Hertz; *Wiener's aggregate entropy*: degree of disorder (i.e. noisiness) of the call, which uses the total energy in a frequency bin over the entire call; *Wiener's average entropy*: mean of the mean entropies of the different time slices of a call.

We selected records according to their quality for these variables. We randomly selected no more than three calls per sequence. A sequence was defined as a series of calls separated by a maximum of 3 s. Females with a sample size of less than five calls were excluded from the analysis. We also excluded some specific types of calls that were not present in the samples of all species (alarm calls) or that had no equivalent in all species (œstrus calls, twits, and cackles). Our sample resulted in 434 calls in 24 Japanese macaques (agonistic context: total number of calls = 79 & mean number of calls per female ± *SD* = 3.30 ± 3.77; affiliative context: 94 & 3.92 ± 4.16; neutral context: 255 & 10.6 ± 5.48), 639 calls in 16 Japanese macaques (agonistic: 118

& 7.38 ± 6.75; affiliative: 59 & 3.69 ± 3.22; neutral: 461 & 28.8 ± 16.0), 700 calls in 13 Tonkean macaques (270 & 20.8 ± 26.3, 226 & 17.4 ± 14.3, 202 & 15.5 ± 8.42), and 696 calls in 19 crested macaques (201 & 10.6 ± 6.61, 297 & 15.6 ± 11.8, 191 & 10.1 ± 7.40).

2.4. Statistical analyses

Statistical analyses were run in *R v 3.5.3* (Core Team 2018). A first analysis focused on the context specificity of calls by assessing the overlap between acoustic structure and social contexts. We followed a 4-step procedure to examine the extent to which the classification of calls by their acoustic structure could correspond to the classification of calls according to social context in each species. We first described the calls by seven acoustic variables. To reduce the dimensionality of the data set and obtain a summary data space with less noise, we applied a Principal Component Analysis (PCA), which allowed to limit correlations between factors that could influence clustering. Before the PCA, we scaled the acoustic variables to obtain a standard deviation of one and a mean of zero using the *R base* function *scale* in each species. The analysis was carried out with the function *PCA* of the package *FactoMineR* (Lê et al. 2008). To balance the contribution of each individual to the creation of the space and give equal weight to each female, we balanced females according to the number of their calls by using the argument *row.w* of the function *PCA*.

In a second step, we performed a hierarchical cluster analysis using the function *hcpc* of the package *factominer* (Sebastien et al. 2008). We set the number of clusters for each species at 9, based on the mean number of broad categories of calls per context in macaques (see Chapter 5). Since our dataset contained different numbers of calls for each social context, we randomly sampled 50 calls per context, so each context had the same probability of occurring in any cluster if they were distributed entirely at random. For example, if the sample was biased towards a particular social context, it was more likely that the clusters were composed of this social context.

In a third step, we measured the extent to which the same acoustically-based cluster of calls could be emitted in different social contexts. We applied information theory to calculate an entropy value for each cluster (see Supplementary material). This value quantitatively expresses the uncertainty in identifying the context associated with a particular signal structure. If there is a strict relationship between the structure of calls and their social context, then each cluster should contain mainly calls belonging to a single context. On the contrary, if the relationship between acoustic structure and social context is looser, the proportions of calls belonging to different contexts within each cluster should be more even. The entropy values of each cluster were then transformed into relative entropy values: the entropy divided by the logarithm of the

number of categories, i.e. the number of social contexts. The relative entropy value closes in on 0 as the cluster approaches a state where it only contains calls from the same social context. The relative entropy value closes in on a maximum (i.e. the log of 3) when the cluster approaches a state where it contains as many calls from each social context. See Supplementary material for more information.

Lastly, we statistically compared the mean relative entropy values of the four species of macaque. We repeated the sampling procedure, clustering procedure, and entropy analysis using bootstraps, with a number of 100 repetitions per species. This resulted in four mean relative entropy values, one for each species, based on 100 random samples. We compared the relative entropy values between species using a linear model (LM). We compared the complete model (i.e. the one with species) to the null (i.e. the one without species) using likelihood ratio tests (LRT) with the function *lrtest* of the package *lmtest* (Zeileis and Hothorn 2002). This made it possible to test whether the species factor had a significant effect. We finally used post-hoc tests to make pairwise comparisons on species using the function *emmeans* of the package *emmeans* (Lenth et al. 2018).

We conducted a second analysis to examine the differentiation of commenting calls. We tested the existence of acoustic differences between interaction, commenting and uncontextualized calls in rhesus, Tonkean, and crested macaques. We performed discriminant function analyses using the function *lda* of the package *MASS* (Venables and Ripley 2002). Because collinearity can bias the results of linear discriminant analysis (Noes & Movik 2001), we removed acoustic variables so that each pairwise Pearson correlation coefficient between acoustic variables was less than 0.7 (Dormann et al. 2012). We, therefore, included the following variables in the discriminant function analysis: duration, Q2 ratio, Q2 frequency, average entropy. To quantify the possible differences between species in terms of acoustic variables, hereafter referred to as *acoustic distance*, we used the function *PermuteLDA* from the package *multiDimBio* (Samuel V. Scarpino et al. 2013). This function determined whether the three categories of calls were at statistically different locations in the multivariate space. It calculated the multivariate distances between the centroids of the call categories and established through a Monte Carlo randomization whether they differed significantly.

3. Results

3.1. Context specificity of calls

The relative entropy value was different between species (LRT $\chi^2 = 178$, $p < 0.001$) (Fig. 1). Post-hoc tests revealed that the values of Tonkean macaques and crested macaques did not

differ significantly (estimate = -0.025 ± 0.011, t = -2.3, p = 0.100). Japanese macaques had a significantly lower value compared to rhesus (estimate = -0.075 ± 0.011, t = -7.0, p < 0.001), Tonkean (estimate = -0.123 ± 0.011, t = -11.5, p < 0.001) and crested macaques (estimate = -0.147 ± 0.011, t = -13.8, p < 0.001). Rhesus macaques had a significantly lower value than Tonkean (estimate = -0.048 ± 0.011, t = -4.5, p < 0.001) and crested macaques (estimate = -0.072 ± 0.011, t = -6.8, p < 0.001).

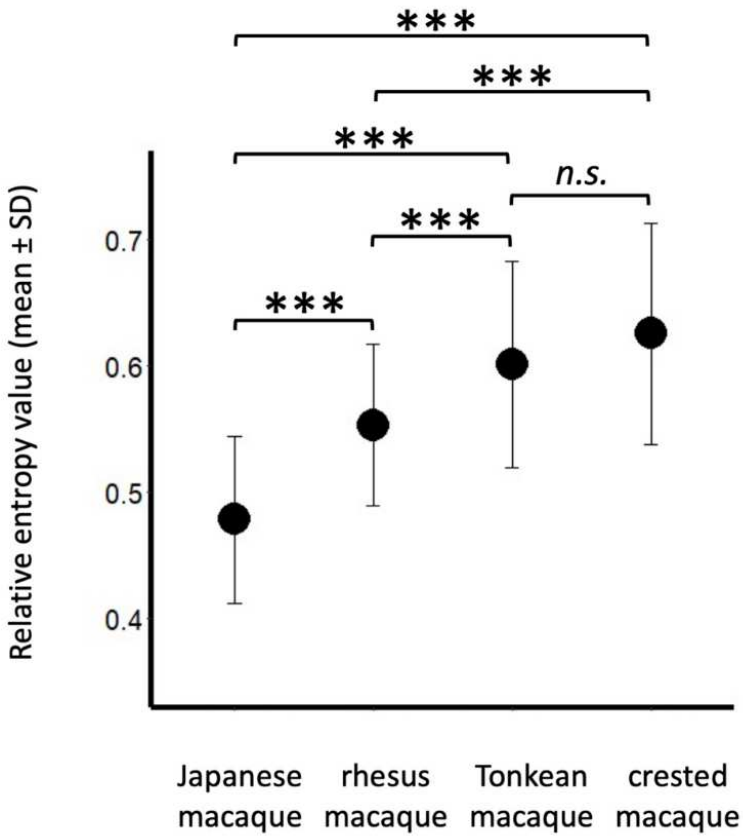


Fig. 1. Degree of association between acoustic structure and social context as measured by relative entropy values in the four species of macaque.

3.2. Form of commenting calls

In rhesus macaques, the multivariate acoustic distance was not significantly different from zero between commenting and uncontextualized calls, meaning that they did not differ significantly according to their acoustic variables (distance = 15.0, p = 0.659). However, the

distance was significantly different from zero between interaction and commenting calls (distance = 483, p = 0.021), and between interaction and uncontextualized calls (distance = 498, p < 0.001), which means that interaction calls differed significantly from commenting and uncontextualized calls according to their acoustic variables (Fig. 2). In Tonkean macaques, the three acoustic distances were significantly different from zero (interaction vs. commenting calls: distance = 486, p < 0.001; commenting vs. uncontextualized calls: distance = 214, p = 0.012; interaction vs. uncontextualized calls: distance = 700, p < 0.001) (Fig. 2). In crested macaques, the acoustic distance was noticeable but not significantly different from zero between interaction and commenting calls, which means that they did not significantly differ (distance = 322, p = 0.185). However, the distance was significantly different from zero between commenting and uncontextualized calls (distance = 322, p = 0.002), and between interaction and uncontextualized calls (distance = 645, p < 0.001), which means that interaction calls differed significantly from commenting and uncontextualized calls (Fig. 2). Lastly, the valence of a proportion of commenting calls (N = 52 over 116) could be unambiguously classified by the ear as agonistic (27.6%) or affiliative (17.2%). The valence of these calls was in most cases (92.3%) congruent with the agonistic or affiliative content of the social interaction attended by the calling bystander.

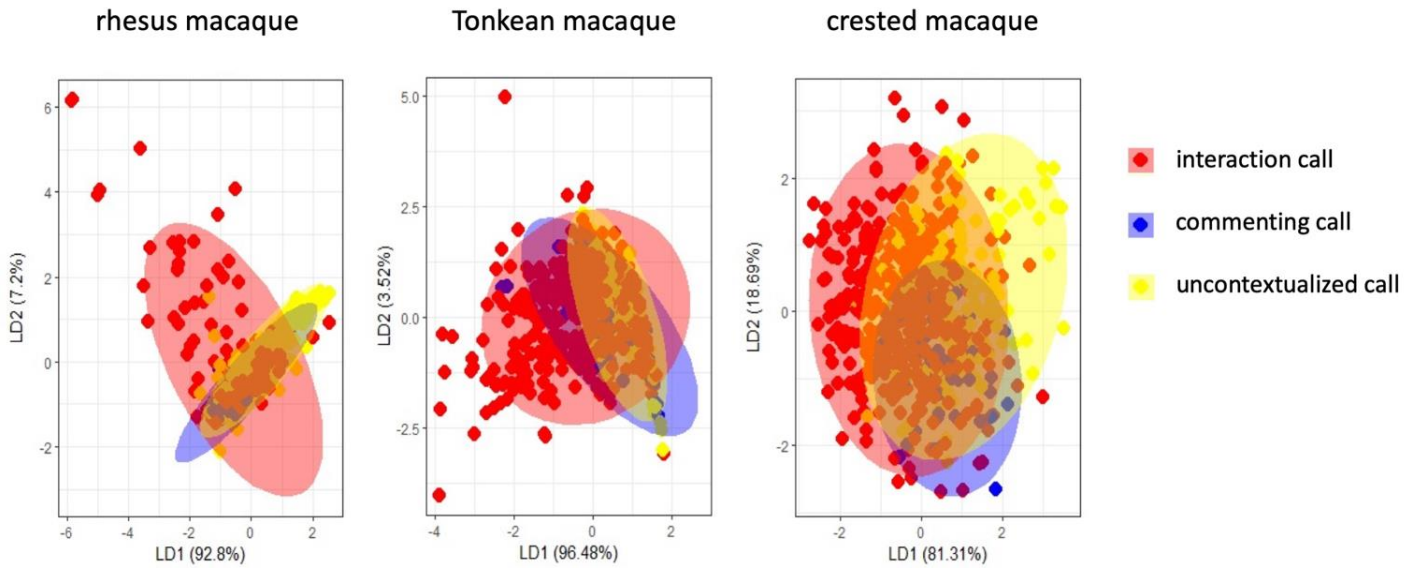


Fig. 2. Acoustic distances between interaction, commenting and uncontextualized calls for three species of macaque: Linear Discriminant Analysis biplot with the three centroids of call categories on the first two linear discriminants (LD1 & LD2). The ellipses correspond to the 95% confidence interval.

4. Discussion

The comparison of several species of macaque revealed significant interspecific differences in the context specificity of their vocal signals, i.e. overlap between acoustic structure and social context and the degree of differentiation of commenting calls. In particular, we found that tolerant macaques had a higher degree of freedom than intolerant macaques in the association between vocal structure and social context. These results have been made possible by the development of quantitative methods based on Shannon's information theory (Chapters 1 & 5).

Analysis of overlap between acoustic structure and social context of call emission showed greater relative entropy values in Tonkean and crested macaques than in Japanese and rhesus macaques. This implies either that the calls emitted in different contexts had closer acoustic structures in tolerant than in intolerant macaques, or that calls having a given valence – agonistic, affiliative or neutral – were used in greater proportions in contexts corresponding to different valences in the former than in the latter species. In both cases, this means that there was more uncertainty in vocal signalling in tolerant macaques than in their intolerant counterparts. The strength of the regularities between the signal and its context of emission determines the extent to which the listener can obtain precise information from the signal; the less context-specific a signal is, the more additional information from the context is needed by the listener to give it meaning (Smith 1965; Seyfarth and Cheney 2003; Wheeler and Fischer 2012). From the degree of freedom between vocal structure and occurrence context, we can deduce the potential range of meanings in the communicative repertoire of a species. The looser association found between structure and context in tolerant macaques indicates that their vocal communication system may involve a greater variety of meanings compared to intolerant macaques.

In intolerant species such as Japanese and rhesus macaques, it can be said that individuals experience quite straightforward social situations. As previously mentioned, dominance and kinship rule their social life, interindividual conflicts most often end in clear winners and losers, and subordinates commonly direct formal signs of submission at higher-ranking individuals (Preuschoft and van Schaik; Thierry 2000, 2007; Rebout et al. 2017). This is consistent with the use of context-specific signals, capable of providing listeners with precise information with only a minimum of contextual cues, as documented by Gouzoules and colleagues (1984, 1998) for rhesus macaque scream vocalizations. By comparison, the outcome of the social interactions of tolerant species such as Tonkean and crested macaques is not easily predictable from their dominance and kinship relationships, they have better skills than intolerant macaques in the

social domain, and they often switch quickly from aggression to flight, protest or reconciliation for example (Thierry et al. 1994; Thierry 2000, 2007; Duboscq et al. 2014; Joly et al. 2017). In such circumstances, the use of signals that are weakly dependent on context leaves a great deal of uncertainty in the information. Flexible calls bring richness in communication, offering a wide range of expression that can allow listeners to better manage ambiguous social situations.

The study of commenting calls lends an additional dimension to these results by examining the ability of individuals to move out of their immediate context and communicate as third parties about their group mates' interactions (Brumm et al. 2005). In rhesus macaques, the vocal performances of interacting individuals were distinct from those not directly involved in social interactions. In contrast, no differences were observed in the acoustic structure of their uncontextualized and commenting calls, indicating that the latter do not convey additional information. In more tolerant species such as Tonkean and crested macaques, interaction calls deviated from commenting calls – albeit non-significantly in crested macaques –, and we found marked discrepancies between uncontextualized and commenting calls. These last calls, therefore, appear as well-differentiated comments from bystanders on outgoing events. Their valence was generally in agreement with the valence of the observed interaction. Not only can the caller alert other group members, but by expressing her/his emotional response remotely while witnessing a social interaction, s/he can also transmit filtered information about its content. There are indications that Tonkean and crested macaques have a particularly strong commitment to the behaviour of others, associated with frequent polyadic interactions (Petit and Thierry 1994, 2000; Petit et al. 2008; Palagi et al. 2014; Puga-Gonzalez et al. 2014). The information conveyed by commenting calls may contribute to this pattern and enhance social cohesion by adding communicative feedbacks at the collective level.

It can be noticed that there is only limited interest in providing specific comments on interactions whose outcome is foreseeable, as is the case with rhesus macaques. On the contrary, when results remain uncertain, such as in more tolerant species, the diffusion of information within the group through circumstantial comments can be beneficial in the same way that food calls spread information on food availability (Hauser and Marler 1993; Clay and Zuberbühler 2009). Moreover, our results point to a possible link between communicative flexibility and emotional expressiveness, in accordance with the motivation-structural hypothesis of Morton (1977), which states that a wide range of sounds corresponds to more points along motivation gradients and rapid changes in motivation. A low degree of association between structure and function in tolerant macaques can allow signallers to gradually move from one call to another, and express a broad spectrum of emotions in a given context (Freeberg et al. 2012a).

Using uncertainty as an indicator of complexity, our results support both predictions of the social complexity hypothesis for communicative complexity regarding the context specificity

of calls, i.e. the degree of overlap between structure and context and the form of commenting calls. Species with a higher degree of uncertainty in social interactions (i.e. social complexity) were also those with a lower degree of association between acoustic structure and social context, and therefore uncertainty in vocal signals (i.e. vocal complexity). This is consistent with the findings of an earlier study where we found that the diversity and flexibility of the acoustic structure of vocal signals was greater in species displaying a higher degree of social complexity (Chapter 5). Taken together, these results show that the vocal signals of more tolerant and socially complex macaques have a greater potential of information than less tolerant and socially complex macaques, thanks to a higher degree of gradation of signals, and a higher degree of freedom in the association between acoustic structure and social context. It should be noted that the causal direction of the social complexity hypothesis is still under discussion (Peckre et al. 2019). Complex social situations may require complex communicative skills, but complex communicative skills may also foster the emergence of complex social situations; these two processes are not mutually exclusive.

The physical structure of the habitat may affect variables such as the frequency or amplitude of auditory signals, for example (Waser and Brown 1986; Hauser 1996), but we know of no variations in the ecological environment of macaques that could explain the interspecific differences we have discovered. It can be added that we have studied the vocalizations of three species in captive settings, and in nature for the fourth, but we found no contrasts between groups that could be attributed to the recording conditions. Phylogenetic relatedness between species is another possible confounding factor. Japanese and rhesus macaques on one side and Tonkean and crested macaques on the other side belong respectively to two different macaque lineages (Chapter 5). One may wonder to what extent this could account for the contrasts observed between the two pairs of species. However, the measurement of acoustic distances between call categories gave rise to cross-species contrasts that could not be explained by phylogenetic relationships between species (chapter 5). Future research should extend the analyses to more groups and species to confirm our current conclusions. It would also be necessary to address vocal signals such as commenting calls through playback experiments to investigate the ability of listeners to attribute meanings to comments having levels of context-specificity.

Supplementary material

from "Tolerant and intolerant macaques differ in the context specificity of their calls and the form of their comments"

We measured an entropy value for each cluster based on the formula of Shannon (1948):

$$H = -\sum_{i=1}^{S} p_i \log p_i$$

h is the Shannon's entropy, *S* the number of social context, and p_i the proportion of calls in the cluster for the context *i*. *H* varies from near zero (one social context is highly predominant in the cluster) to a maximum value of log *S* (the cluster is composed of the three social context in the same proportion)

For comparative purposes, we used the relative index (Pielou 1969; Peet 1974):

$$h = \frac{H}{H_{max}}$$

H_{max} is the maximal value of *H*, i.e. log *S*

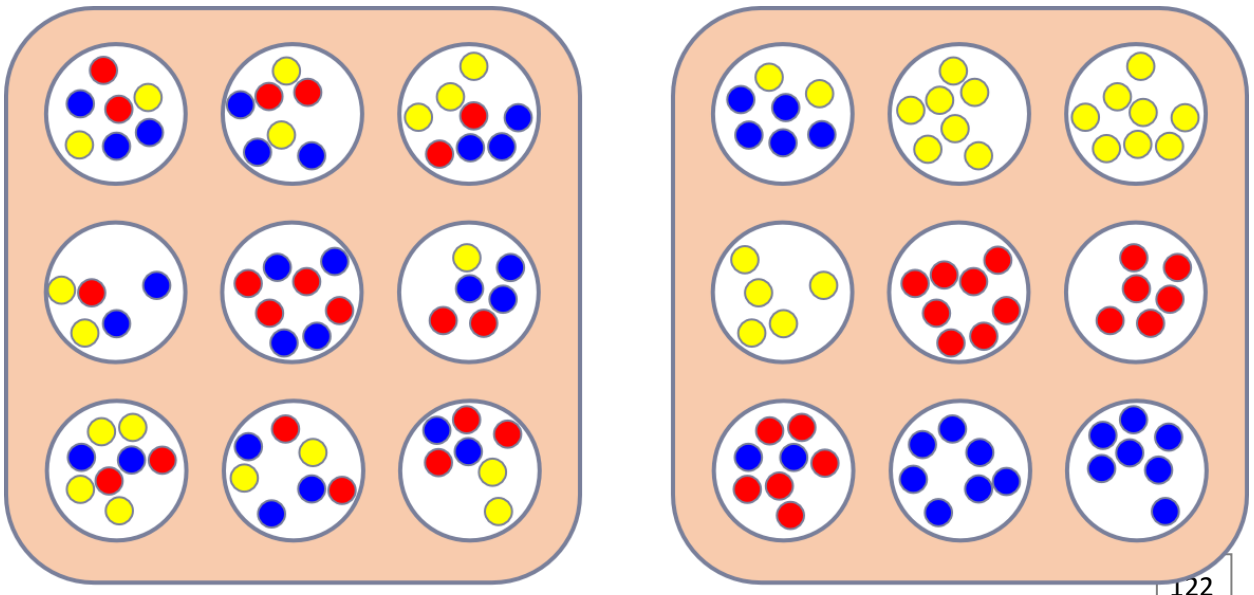
The calculation of the relative entropy index is illustrated in Table 1. The application of the formula can be seen in the row General case. If a cluster is composed of calls from a single context, the entropy and the relative entropy are equal to 0 by convention (case 2). If a cluster is composed of calls from two contexts only, the entropy is calculated on these two contexts, which allows to avoid applying logarithms on null values, but still allows comparisons because thereafter the entropy value is divided by the logarithm of three (case 1).

Table 1. Examples of calculation for entropy (*H*) and relative entropy (*h*).
Figures are arbitrary, they are given for illustrative purposes.

	Agonistic context	Affiliative context	Neutral context	Calculation
General case	0.5	0.25	0.25	$H = -0.5 \log 0.5 - 0.25 \log 0.25 - 0.25 \log 0.25 = 1.5$ $h = H / \log 3 = 0.95$
Case 1	0.6	0.4	0	$H = -0.6 \log 0.6 - 0.4 \log 0.4 = 0.97$ $h = H / \log 3 = 0.61$
Case 2	1	0	0	$H = 0$ $h = 0$

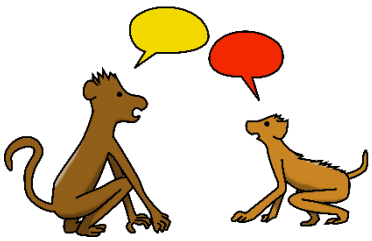
The diagrams in Figure 1 illustrates two extreme cases of clustering results. Each of the nine large circles represents a cluster. Each cluster consists of a group of calls (small circles) identified according to the acoustic structure of these calls. Calls are coloured according to their context of occurrence (three colours for three social context). In the case of a high relative entropy value (1), each context is distributed over a large number of clusters. In the case of a low relative entropy value (2), each context is limited to a small number of clusters, and each cluster consists mainly of one context. When relative entropy is low, knowing the cluster to which a call belongs provides reliable information about the context in which it was probably emitted. This is not true when the relative entropy is high.

Fig. 1. Diagrams illustrating the method.

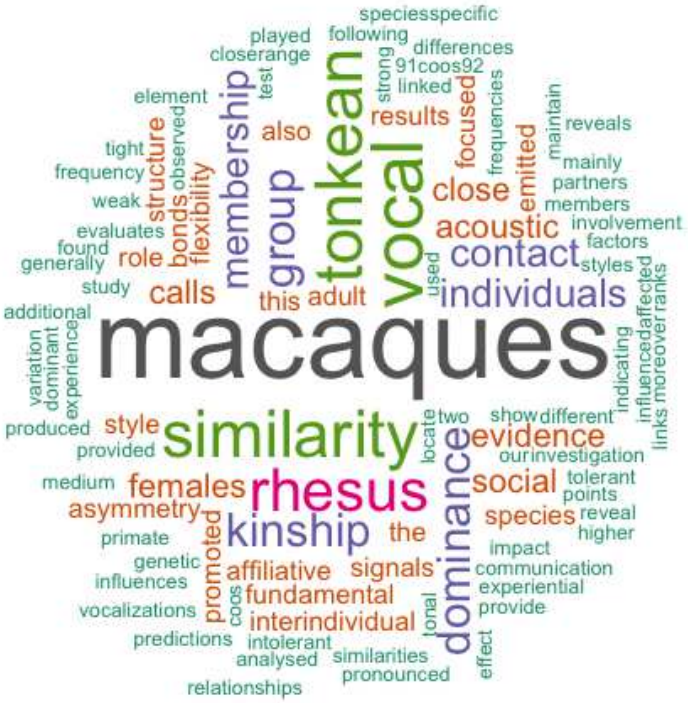


(1) High relative entropy value

(2) Low relative entropy value



CHAPTER 7
Differential patterns of vocal similarity in tolerant and intolerant macaques



Differential patterns of vocal similarity in tolerant and intolerant macaques

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Abstract

The investigation of vocal similarity between individuals has provided evidence of the flexibility of communication signals. This study evaluates the impact of group membership, affiliative bonds, kinship and dominance on acoustic similarity in two primate species with different social styles, intolerant rhesus macaques and tolerant Tonkean macaques. We focused on the fundamental frequencies of the contact calls emitted by adult females. Close kinship promoted vocal similarity between individuals in both species, and also group membership in Tonkean macaques, indicating the involvement of experiential and/or genetic factors. In rhesus macaques more similarities were observed between partners with strong or weak dominance asymmetry than between those with medium asymmetry, which again points to the role of experience. No evidence was found that dominance influences vocal similarity in Tonkean macaques. Our results provide additional evidence to the flexibility of vocal signals produced by macaques, and reveal that it is influenced by social style.

Keywords

Learning, vocal communication, dominance, social style, primate.

1. Introduction

For some time now, the literature on animal vocal communication has tended to split animals into two categories, namely vocal 'learners' and 'non-learners'. While the former learn species-specific acoustic structures from conspecific models and have an extensible repertoire (e.g., songbirds, cetaceans, humans) (Snowdon & Hausberger, 1997; Wilbrecht & Nottebohm, 2003; Janik, 2014), the vocal performances of the latter were considered to be driven by a strong genetic determinism that restricts their repertoire to a limited number of call types, as reported in non-human primates (Newman & Symmes, 1982; Hammerschmidt & Fischer, 2008). However, there is now evidence that social influences induce multiple adjustments in the structure of these call types, and that their usage can also be socially learned, particularly in non-human primates (Snowdon, 2017; Cheney & Seyfarth, 2018). A number of studies have shown significant levels of vocal flexibility in monkeys and apes, meaning that the acoustic structures and usages of calls can be modified to some extent through learning (Lemasson et al., 2013; Gruber & Grandjean, 2017; Lameira et al., 2017).

The study of vocal similarity and convergence has provided compelling evidence of feedback from the social environment acting upon communication signals. Vocal convergence is a process in which the acoustic properties of the calls emitted by different individuals come to match over time (Snowdon & Hausberger, 1997). It increases acoustic similarity within communities and promotes divergence between communities. This has been reported in songbirds, cetaceans, elephants, bats and primates (Tyack, 2008), but also more recently in gazelles (*Gazella subgutturosa*), goats (*Capra hircus*) and mice (*Mus musculus*), i.e. species that are not considered to possess particular learning abilities (Arriaga et al., 2012; Briefer & McElligott, 2012; Volodin et al., 2014).

Convergence may arise at the interaction level during vocal exchanges between conspecifics. In vocal exchanges, callers modify the acoustic structure of some of their calls to match those of others. This is reported among female Japanese macaques (*Macaca fuscata*) (Sugiura, 1998), and between mothers and their offspring in gibbons (*Hylobates agilis*) (Koda et al., 2013). In chimpanzees (*Pan troglodytes*), males forming alliances match frequency modulation patterns when chorusing together (Mitani & Gros-Louis, 1998). Moreover, individuals can converge or diverge vocally depending on the context. In a study of female Diana monkeys (*Cercopithecus diana*), the acoustic structure of contact calls diverged between group mates when travelling in a habitat with poor visibility, and calls converged during vocal exchanges (Candiotti et al., 2012). It is worth mentioning that phonetic convergence – or divergence – is also used to signal attitudes between human interlocutors during conversations. This phenomenon is known as vocal accommodation and regulates social inclusiveness (Giles et al., 1991).

Vocal convergence can also arise over the long term from the social relationships between two individuals. In pygmy marmosets, pairing with a new mate led to modifications in trill structure within six weeks, resulting in more homogeneous calls between mates (*Cebuella pygmaea*) (Snowdon & Elowson, 1999). In Campbell's monkeys (*Cercopithecus campbelli*) and bonobos (*Pan paniscus*), two rather tolerant species (Lemasson et al., 2006; Gruber et al., 2016), greater similarities were observed between the contact calls of partners that had stronger affiliative bonds (Lemasson et al., 2011) and were same-age peers (Levréro et al., 2018), respectively, and convergence patterns reflected the changes that occurred in social relationships over the years (Lemasson & Hausberger, 2004). In Japanese macaques, a dominance-oriented species, vocal similarity in contact calls was influenced by dominance relationships rather than by affiliative bonds: the higher the rank difference within dyads, the higher the acoustic similarity. This led authors to propose that vocal convergence is a strategy through which subordinates copy the vocalizations of higher-ranking individuals (Lemasson et al., 2016). It is also reported that vocal convergence occurs more frequently between partners of different social status in humans, with the less powerful individual being more likely to modify his/her vocal expression and converge on the other (Gregory & Webster, 1996; Anderson et al., 2003; Pardo et al., 2012).

Vocal similarity has been reported at the group level for contact calls in Japanese macaques and pant hoots in chimpanzees (Crockford et al., 2004; Tanaka et al., 2006). In the latter species, the males of neighbouring communities develop group-specific pant hoots: neighbouring communities diverged more from each other than from another, geographically distant community (Crockford et al., 2004). The merging of two groups of chimpanzees in captivity induced convergence in the acoustic structure of food grunts, with the newly introduced individuals adopting the structure of the host group (Watson et al., 2015). Interpopulation variations in vocal patterns have also been described in several primate species (Japanese macaques: Green, 1975; Barbary macaques [*Macaca sylavanus*]: Fischer et al., 1998; saddle-back tamarins [*Saguinus fuscicollis*]: Hodun et al., 1981; red-bellied tamarins [*Saguinus labiatus*]: Maeda & Masataka, 1987; chimpanzees: Mitani et al., 1992; pygmy marmosets: de la Torre & Snowdon, 2009). According to the 'password' or 'badge' hypothesis, shared calls can indicate membership of a given community (Feekes, 1982; Snowdon & Hausberger, 1997; Wilkinson & Boughman, 1998).

When seeking evidence of similarity and convergence, a main issue is to check whether vocal matching between individuals can simply be a consequence of genetic proximity. Vocal production is strongly affected by genetic inheritance (Hammerschmidt & Fischer, 2008), as indicated by hybridization or cross-fostering experiments (Geissmann, 1984; Owren et al., 1993). A study in mandrills (*Mandrillus sphinx*) showed that the acoustic structure of contact

calls was more similar between relatives than among unrelated individuals, and this similarity was likely due both to genetic relatedness and vocal copying (Levréro et al., 2015).

While the general structure of a call may be inherited, fine acoustic components may be influenced by the environment. As an example, the arch structure of contact calls appears genetically determined in rhesus macaques (*Macaca mulatta*) (Owren et al., 1993), but the duration and amplitude of the frequency modulation, as measured in Japanese macaques, vary significantly from one context to another in any given individual (Koda, 2004). Another study on rhesus macaques showed closer similarities between the contact calls of females belonging to the same social group and matriline than those emitted by females from different social groups and matrilines, yet the authors did not find any evidence of an effect of the degree of genetic relatedness, and concluded that similarities in vocal structures between individuals was a consequence of familiarity between them (Pfefferle et al., 2016). Likewise, the authors of three other studies also argued that acoustic similarity in contact calls was not related to genetic relatedness (Japanese macaques: Tanaka et al., 2006; Campbell's monkeys: Lemasson et al., 2011; bonobos: Levréro et al., 2018).

The present study aimed to investigate the effect of group membership, kinship and social relationships on vocal similarity in macaques. Wide cross-species variation in the social style of macaques makes it possible to assess the influence of dominance and kinship on vocal similarity, and thus evaluate the role played by the social environment in the evolution of communicative abilities (Freeberg et al., 2012; Gustison et al., 2012; Maciej et al., 2013). All macaques form linear hierarchies and live in groups that are structured in matrilines, i.e. subgroups of relatives that are linked by maternal descent (Thierry, 2011). Species such as rhesus and Japanese macaques are characterized by strong social intolerance, meaning that they display a steep gradient of dominance coupled with conspicuous submission signals, and a strong preference for kin partners. Other species, like Tonkean macaques (*Macaca tonkeana*), show higher levels of tolerance, which corresponds to moderate power asymmetries, a high propensity to regulate conflicts through affiliative behaviours, and a low degree of nepotism (Thierry, 2007; Balasubramaniam et al., 2012; Rebout et al., 2017). The covariation hypothesis states that the different patterns of social styles are interconnected, and that any significant variation of a single character can induce a set of correlated changes in other traits (Thierry, 2007). We can therefore expect the influence of dominance and kinship on vocal similarity to be modulated by cross-species variations in social style.

We focused on contact calls, or ‘coos’. In macaques these close-range vocalizations are mainly used to locate group members and maintain vocal contact between them, and they have a tonal acoustic structure in which the fundamental frequency is generally the dominant

element. We analysed the inter-individual acoustic variation of coos emitted by females in rhesus and Tonkean macaques to test the following predictions: (1) Vocal similarity should be higher between individuals linked by group membership, close kinship and/or tight affiliative bonds than between individuals not having such links, (2) The effect of kinship and dominance relationships on vocal similarity should be more pronounced in rhesus macaques than in Tonkean macaques.

2. Methods

2.1. Subjects

Behavioural observations and acoustic recordings were carried out in 13 adult females from four groups of Tonkean macaques, and 12 adult females from two groups of rhesus macaques. All females were at least five years old, captive born, and had known maternal kin relationships.

Tonkean macaques belonged to a population originating from a stock imported to France in 1972, and since divided into several groups throughout the years (Table 1) (Herrenschmidt, 1977; Thierry et al., 1994). Tonkean group B consisted of 15 individuals including 4 adult females and was housed in a 120 m², 4 m high enclosure at the Orangerie Zoo of Strasbourg, France. The other three Tonkean groups (C, D, E) were housed in enclosures approximately 500 m² and 5 m high at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy (De Marco et al., 2014). These groups consisted of 16, 15 and 9 individuals including 4, 3 and 2 adult females, respectively (Table 1).

Rhesus macaques belonged to a population originating from a stock imported from India to The Netherlands in the seventies (Neefe et al., 1975; Doxiadis et al., 2013). The two groups of rhesus macaques were founded in 2004. They were housed in enclosures approximately 210 m² and 3 m high at the Biomedical Primate Research Center in Rijswijk, The Netherlands. They were composed of 35 and 31 individuals including 10 and 6 adult females, respectively (Table 1).

All enclosures were furnished with wooden structures, perches and ropes. Animals were fed commercial monkey diet pellets, complemented with fresh fruit and vegetables. Water was available *ad libitum*. This study respected the legal requirements and guidelines of the Italian, French and Dutch governments, and followed ASAB/ABS guidelines for the treatment of animals in behavioural research.

Table 1. Information about groups and subjects.

Group	Dates of group foundation and study	Composition of group[1]	Name and age in years of focal females[2]	Percentage of maternal relatedness between focal females[3]
rhesus group A	founded in 2004 studied in July–October 2016	10 adult females, 3 adult males, 22 immatures	Pip (14), But (13), Isa (11), Nil (10), Hoe (10), Wie (9), Lok (7), Aus (6), Mon (5), Pan (5)	43%
rhesus group B	founded in 2004 studied in July–October 2016	6 adult females, 1 adult male, 24 immatures	Tro (13), Plo (12), Hat (10), Jah (8), Kwe (7), Ymi (6)	27%
Tonkean group B	founded in 1978 studied in February–May 2016	4 adult females, 6 adult males, 5 immatures	Gil (27), Gai (9), Giu (9), Lis (5)	33%
Tonkean group C	founded in 2005 studied in September–December 2014	4 adult females, 4 adult males, 8 immatures	Pal (13), Sop (11), Pam (8), Pap (6)	50%
Tonkean group D	founded in 2007 studied in March–May 2015	3 adult females, 5 adult males, 7 immatures	Sib (12), Tet (11), Tan (11)	0%
Tonkean group E	founded in 2009 studied in September–December 2014	2 adult females, 3 adult males, 5 immatures	Nin (15), Nif (9)	100%

[1] Immature: less than 5-year, adult: at least 5-year old (De Marco et al., 2014).
[2] Age at the beginning of data collection.
[3] Percentage of maternal relatedness (mother-daughter, sister-sister) between females calculated on the total number of relationships between females.

2.2. Data collection

We carried out observations in outdoor enclosures between 09:30 and 16:30 from September 2014 to May 2016 in Tonkean macaque groups, and from July 2016 to October 2016 in rhesus macaque groups (Table 1). We used random focal samples to record vocalisations (including coos) in adult females. Sample duration was 15 min in rhesus groups and Tonkean group B, and 10 min in Tonkean groups C, D and E. This resulted in 12.7 ± 0.7 hours of focal sampling per subject in rhesus macaques (total: 203.25 hours) and 13.6 ± 3.2 hours in Tonkean macaques (total: 177.4 hours). We also recorded instantaneous samples of contact sitting and social grooming every 10 minutes.

Observers also used all occurrences sampling to collect data for supplantations (an individual approaches another who leaves immediately) and unidirectional conflicts (an individual threatens or attacks another who flees or submits) in the studied groups. As the majority of conflicts in Tonkean macaques were bidirectional, we collected additional data about agonistic interactions during competition tests in this species (see Thierry et al., 1994). According to breeding conditions, we recorded all occurrences of supplantations and unidirectional conflicts during food distribution in groups C, D and E (20-min periods every morning before the focal sampling), or around a single source of orange juice in group B (seven 2-hr tests) (see Thierry et al., 1994).

Recordings of vocalizations were made with a Marantz (Eindhoven, The Netherlands) PMD 661 recorder (WAV format, sampling frequency: 44 100 Hz, resolution: 16 bits) and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. A lavalier microphone (TCM 160, Meditec, Singapore) was connected to the recorder to add comments about the context of call emission. To ensure caller identification and sound quality, only coos emitted by individuals located within 5 meters of the recorder were considered for analysis. Audacity software (version 2.0.5) was used to split the recordings for each coo, thus creating separate audio files to analyze calls. Records were of poor quality for one female (Isa) in rhesus macaques and they were removed from the analysis. Sampling produced an average of 14.5 ± 11.6 calls with good acoustic quality per female (Tonkean macaques: 15 ± 9.9 calls; rhesus macaques: 14 ± 13.7 calls).

2.3. Acoustic analysis

We applied the ANA software (Richard, 1991) to calculate a dyadic acoustic similarity index that expresses the degree of similarity of two given calls. Spectrograms were drawn with a Fast-Fourier Transformation using a window size of 256 and an overlap of 128. Recordings were downsampled at 11 025 Hz. A single investigator who had not been informed about the hypotheses underpinning the study, computed the similarity index for each pair of calls made by two different females. This index compares the shape of the frequency modulations of two calls, based solely on the patterns of the fundamental frequency (for other applications of this method in guenons, gibbons and macaques, see Lemasson et al., 2011, 2016; Candiotti et al., 2012; Koda et al., 2013). Every call emitted by a female was matched with every call emitted by all other females. Given the frequency modulation pattern of macaques' coo calls, this procedure allows the computation of a single global similarity index rather than making a relatively subjective selection of specific acoustic parameters that are not always representative of the overall acoustic complexity. In a first step, the amplitude of all the sampled calls was homogenised; all calls were automatically boosted to the same maximum in a proportional way to ensure comparable amplitude scales and prevent any potential bias due to differences in

recording quality. We then extracted the fundamental frequency to discard background noise and harmonics. In a third step, we ran an automatic calculation, based on pixel by pixel comparisons between spectrograms. Each pixel was associated with a grey value ranging from 0 (white) to 255 (full black). If one or both compared pixels had a grey value of zero, we attributed a score of 0. If the grey values of the two compared pixels differed by less than 16, we attributed a score of 2. We attributed a score of 1 to other combinations. (The choice to set the threshold at 16 was admittedly somewhat arbitrary at the outset. However, the validity of this choice was subsequently confirmed in all comparable published works with a broad range of non-human primate species including macaques (Lemasson et al., 2011, 2016; Candiotti et al., 2012; Koda et al., 2013), so this threshold was retained.) We computed a similarity index ranging between 0 and 1 by dividing the total of all scores by the total number of pixels in both spectrograms. The algorithm then carried out the same operation for all possible superpositions by comparing spectrograms of two individuals along the time axis. This generated similarity indices for every possible superposition (Lemasson et al., 2011). Once all possible superpositions had been compared, the algorithm determined the highest similarity index for the two spectrograms. Examples of comparisons are illustrated in Figure 1.

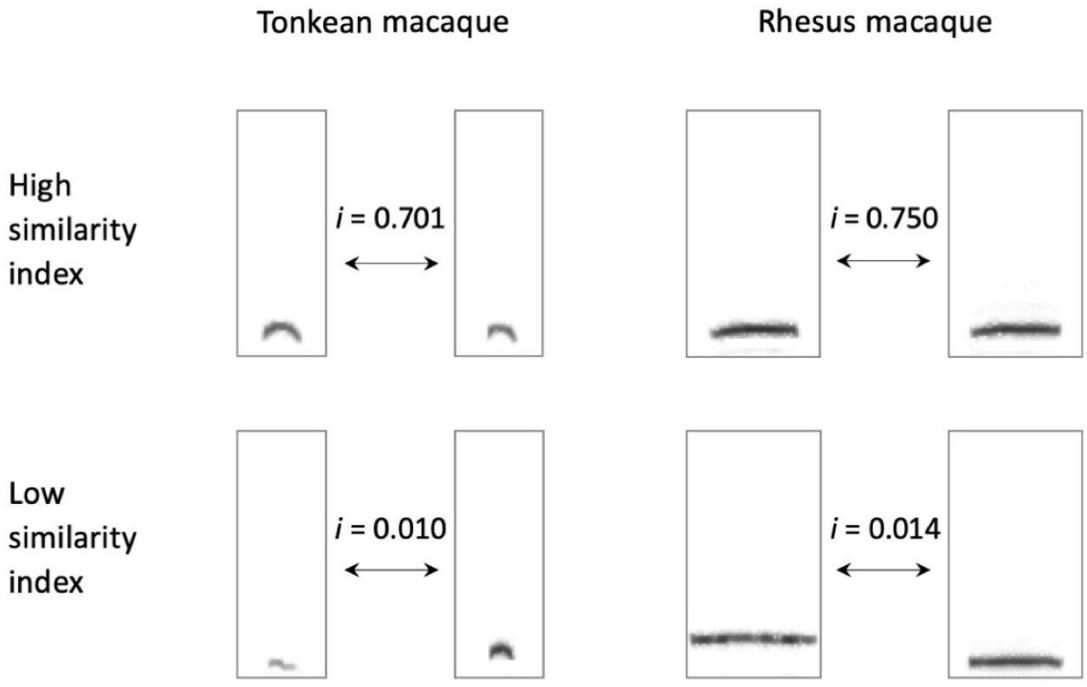


Fig. 1. Examples of spectrograms (frequency as a function of time): two-by-two comparison of coos from different individuals and corresponding dyadic acoustic similarity indices *i* in Tonkean and rhesus macaques.

2.4. Assessment of kinship and social relationships

We assessed kinship based on the coefficient of maternal relatedness, computed from the pedigree data for each pair of subjects. Pairs were labelled as *closely related* when they involved sisters or mother/daughter, or *distantly related* when no such ties were involved (see Table 1). In a first step, we assessed the strength of the affiliative bond in each pair of group members by dividing the number of instantaneous samples involving an affiliative contact (social grooming, contact sitting) between partners by the total of number of instantaneous samples. In a second step, we attributed pairs to two categories of equivalent size, *tightly* and *loosely affiliated*, according to bond strength values.

We assessed the dominance ranks of individuals in each group using supplantations and unidirectional conflicts. We applied SOCPROG software (Whitehead, 2009) to matrices built from agonistic interactions to rank individuals (excluding those less than 1-yr old as dominance rank is meaningless for them) in group dominance hierarchies. The linearity of hierarchies in all groups was verified using the linearity index h' (de Vries et al., 1993), with the following results: Tonkean group B: $h' = 0.51$, $p = 0.004$, Tonkean group C: $h' = 0.77$, $p < 0.001$; Tonkean group D: $h' = 0.64$, $p < 0.001$; Tonkean group E: $h' = 1$, $p = 0.023$; rhesus group A: $h' = 0.35$, $p = 0.003$; rhesus group B: $h' = 0.25$, $p = 0.030$). Individuals could then be attributed to three dominance categories (*high-*, *medium-* and *low-rank*) containing an equivalent number of group members, and we calculated a dominance delta for each pair of subjects: $\Delta = 0$, same dominance category; $\Delta = 1$, difference of one dominance category; $\Delta = 2$, difference of two dominance categories.

2.5. Statistical analyses

We performed Linear Mixed Models (LMM) using *R 3.4.0* (R Core Team, 2017) and the package *lme4* (Bates et al., 2015) to test the effect of social factors on the inter-individual acoustic similarity of coos. The identity of focal females was included as a random factor. As groups of Tonkean and rhesus macaques differed in size, pairwise comparisons of inter-individual acoustic similarity indices resulted in an unbalanced dataset and thus precluded direct cross-species comparisons using statistical interactions. We therefore ran separate models for each species.

We first built models focusing on the effect of group and kinship in each species. The target variable was the dyadic acoustic similarity index. Predictor variables were the group (same vs. different group) and maternal relatedness (closely vs. distantly related); the age difference between females was also included due to its possible effect on acoustic variability (Ey et al.,

2007). We then built models focusing on the effect of social relationships: dominance and affiliative bonds. The target variable was the similarity index. Predictor variables were the dominance delta (0,1 or 2), affiliative bonds (tight vs. loose pairs), and the age difference between females. Maternal relatedness was also included as a random factor in the later models to control for a possible interaction with the dominance delta.

We checked that there was no significant collinearity between predictor variables (variance inflation factor below 3 for all variables). Because several predictor variables could influence target variables, candidate sets of models were evaluated using an information-theoretic approach. Suitable predictors were selected, then the *model.avg* function of the package *MuMIn* (Barton, 2016) was used to investigate their different combinations (Burnham & Anderson, 2002). The level of support was determined for each model through second-order Akaike's Information Criterion (AICc). We applied the procedure of Burnham and Anderson (2002) to define a 95% confidence set of model candidates: we summed the Akaike weights from the largest to the smallest until their sum was equal to or just above 0.95; candidate models were those with a weight sum below 0.95, plus the first model that attained or exceeded 0.95 (Burnham & Anderson, 2002: p. 169). When the confidence set contained more than one candidate model, the model with the largest number of variables was retained as the best one since it was the most explicative model. Residuals were checked visually for normality and homoscedasticity using the package *RVAideMemoire* (Hervé, 2017). Once the best-fitting models had been identified, we determined the significance of effects with the Student's test provided by the package *lme4* (Bates et al., 2015). Post-hoc analyses based on Tukey corrections were run using the package *multcomp* (Hothorn et al., 2008) to assess the effects of factors with more than two conditions. Mean values and standard deviations were estimated for the different factor conditions using the package *effect* (Fox, 2003).

3. Results

3.1. Effect of group and kinship

In Tonkean macaques, the confidence set for the best model candidates contained a single model which included group and kinship variables. (Table 2, Tonkean model 1). Student's tests revealed that females belonging to the same group had higher similarity indexes than those of females in different groups (same group: estimated mean ± SD = 0.276 ± 0.015, different groups: 0.263 ± 0.015, estimate $_{\text{same vs. different}}$ ± SE = 0.013 ± 0.003, $t = 4.67$, $p < 0.001$), and that females that had a close kinship relation had a higher acoustic similarity index than others (closely related: 0.284 ± 0.015, distantly related: 0.264 ± 0.015, estimate $_{\text{close vs. distant}}$ ± SE = 0.020 ± 0.005, $t = 4.30$, $p < 0.001$) (Fig. 2).

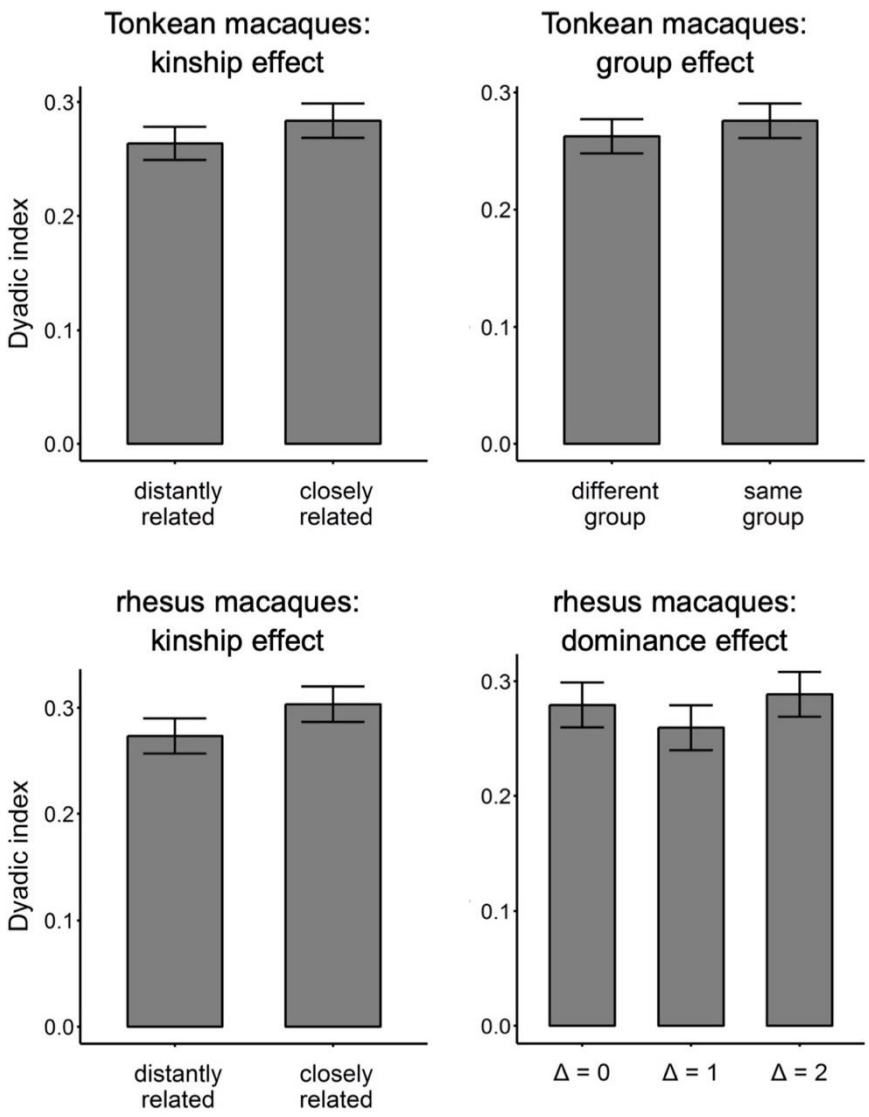


Fig. 2. Results of linear mixed models: kinship and group effects in Tonkean macaques; kinship and dominance effects in rhesus macaques (means and standards deviations).

The confidence set for rhesus macaques contained a single model which included age and kinship difference variables (Table 2, rhesus model 1). Student's tests showed that the acoustic similarity index decreased as the age difference between females increased (estimate ± SE = -0.003 ± 0.0002, t = -13.1, $p < 0.001$). They also revealed that females that had a close kinship relation had a higher similarity index than females with more distant relationships (closely related: 0.303 ± 0.016, distantly related: 0.273 ± 0.016, estimate $_{\text{close vs. distant}}$ ± SE = 0.030 ± 0.002, t = 16.7, $p < 0.001$) (Fig. 2).

The effect of kinship, calculated from the ratio between estimate of effect and intercept in the model, was equal to 0.074 in Tonkean macaques and 0.104 in rhesus macaques.

Table 2. Linear mixed models for group and kinship in Tonkean and rhesus macaques, ranked by the Akaike Information Criterion (AICc): estimates for quantitative effects, presence (+) for qualitative effects, and AICc computations.

Models	Group	Kin-ship	Age diff-erence	Inter-cept	df	logLik	AICc	Delta	Weight	Weight sum
Tonkean macaques										
Model 1	+	+		0.261	6	10323.4	-20634.7	0	0.967	0.967
Model 2	+			0.273	5	10318.6	-20627.2	7.55	0.022	0.989
Rhesus macaques										
Model 1		+	-0.003	0.288	6	23184.5	-46357.1	0	0.998	0.998
Model 2	+	+	-0.003	0.287	7	23179.5.	-46344.9	12.15	0.002	1

3.2. Effect of dominance and affiliative bonds

In Tonkean macaques, the confidence set contained a single model. This was the null model, and was not investigated further (Table 3, Tonkean model 1).

In rhesus macaques, the confidence set contained two models, and the best model included the dominance delta (Table 3, rhesus model 1). Post-hoc tests revealed that females that differed by two dominance categories (Δ = 2: 0.289 ± 0.019, Δ = 0: 0.279 ± 0.019, Δ = 2, i.e. high- and low-rank) had a higher similarity index than dyads from the same dominance category (Δ =0) (estimate $_{\Delta=2 \text{ vs. } \Delta=0}$ ± SE = 0.009 ± 0.003, t = 3.49, p = 0.001) or dyads that differed by one dominance category (Δ = 1) (Δ = 2: 0.289 ± 0.019, Δ = 1: 0.260 ± 0.020, estimate $_{\Delta=2 \text{ vs. } \Delta=1}$ ± SE = 0.029 ± 0.007, t = 4.19, p < 0.001). Females belonging to the same dominance category (Δ = 0) had a higher index than females that differed by one dominance category (Δ = 1) (Δ = 1: 0.260 ± 0.020, Δ = 0: 0.279 ± 0.019, estimate $_{\Delta=1 \text{ vs. } \Delta=0}$ ± SE = -0.020 ± 0.007, t = -2.98, p = 0.007) (Fig. 2).

4. Discussion

Results show that close kinship promoted vocal similarity between adult females in Tonkean and rhesus macaques. Moreover, vocal similarity was affected by group membership in Tonkean macaques but not in rhesus macaques, and also by inter-individual differences in dominance ranks in rhesus macaques but not in Tonkean macaques. This reveals the role played by species-specific social style in the structure of contact calls.

Table 3. Linear mixed models for dominance and affiliative bonds in Tonkean and rhesus macaques, ranked by the Akaike Information Criterion (AICc): estimates for quantitative effects, presence (+) for qualitative effects, and AICc computations.

Models	Domin-ance delta	Affil-iative bond	Age differ-ence	Intercep t	df	logLik	AICc	Delt a	Weight	Weight sum
Tonkean macaques										
Model 1				0.300	5	2267.5	-4525.0	0	0.981	0.981
Model 2		+		0.301	6	2264.3	-4516.5	8.41	0.015	0.996
Rhesus macaques										
Model 1	+			0.279	7	10819.3	-21624.6	0	0.559	0.559
Model 2				0.274	5	10817.0	-21624.0	0.51	0.425	0.984
Model 3		+		0.271	6	10814.5	-21617.0	7.60	0.012	0.996

As predicted, close kinship ties promoted vocal similarity in the contact calls of females: sisters and mothers-daughters resembled one another more than other females in both species. Kinship is a basic tenet of macaque social organization, and although the degree of nepotism varies according to species, all macaque societies are organized along strong matrilines (Thierry, 2011). By contrast, nepotism is less marked in guenons, as seen in female Campbell's monkeys and, correspondingly, no effect of kinship on the acoustic structure of their contact calls has been reported in this species (Lemasson & Hausberger, 2004). It should be added that we did not find any significant effect of affiliative bonds on acoustic similarity. As the number of adult females in each of the studied groups was limited, it may be that many of them were able to maintain good social relationships, making it impossible for us to appreciate the role of social affinities in vocal production. Note that the number of females in the study groups was comparable to those found for macaques in the wild (e.g., Chopra et al., 1984; Pombo et al., 2004; Riley, 2007; Kumar et al., 2013). We additionally found that coos were more similar within groups than between them in Tonkean macaques. A number of studies have reported variations in primate vocalizations at the population level (see Introduction), but few have reported an effect of group membership on acoustic similarity among non-human primates (Crockford et al., 2004; Tanaka et al., 2006).

As in other studies, it is difficult to disentangle the experiential and/or genetic factors responsible for the effects of kinship and group membership. It is possible that the resemblance between close relatives had some genetic basis. Although the occurrence of genetic drift is unlikely across a small number of generations, a founder effect cannot be excluded. However, previous studies did not find an effect of genetic inheritance on the fine acoustic components of coos (Lemasson & Hausberger, 2004; Lemasson et al., 2006, 2016) which are more likely influenced by social patterns. It is known that learning can contribute to vocal convergence (Tanaka et al., 2006; Lemasson et al., 2011; Levréro et al., 2015; Pfefferle et al., 2016). Following the merging of individuals, some vocalizations of group- or pair-members came to converge within a period as short as three years in chimpanzees (food grunts: Watson et al., 2015), or even months or weeks in Campbell's monkeys (agonistic, affiliative & contact calls: Lemasson & Hausberger, 2004) and pygmy marmosets (trills: Snowdon & Elowson, 1999). Most of the macaque groups in the present study were founded relatively recently, and vocal copying between individuals may explain a substantial part of the membership effect found in the acoustic structure of female coos.

In rhesus macaques, the vocal similarity of contact calls was influenced by the position of females in the social hierarchy: the coos emitted by partners displaying a strong dominance asymmetry exhibited more similarity than those of females with less dominance difference. This is consistent with the results of a previous study in another intolerant species, the Japanese macaque, which led the authors to assume that subordinate females tend to converge with the voices of leaders (Lemasson et al., 2016). In rhesus macaques, however, the coos of females belonging to the same dominance category also appeared to be more similar than those of females that differed by one dominance category. This can be considered a case of convergence where the development of vocal similarity would be favoured by the low levels of social competition between these individuals and between those that are separated by strong differences in dominance ranks, whereas it would be hindered by heightened competition between group members with closer dominance ranks (see Belzung & Anderson, 1986). Further research will be needed to pinpoint the origin of this non-linear effect of female dominance status. It is noteworthy however that this effect cannot be explained by mere genetic inheritance, reinforcing the argument that social relationships influence the acoustic structure of coos.

Contrary to results in rhesus and Japanese macaques (Lemasson et al., 2016), testing the effect of dominance categories on the acoustic similarity of female coos did not yield any significant effect in Tonkean macaques. This result is in accordance with the social style of this species. Whereas rhesus and Japanese macaques display strong power asymmetries between individuals, Tonkean macaques are characterized by relaxed dominance relationships. Interestingly, a similar result was found for the chorused calls of subordinate male chimpanzees,

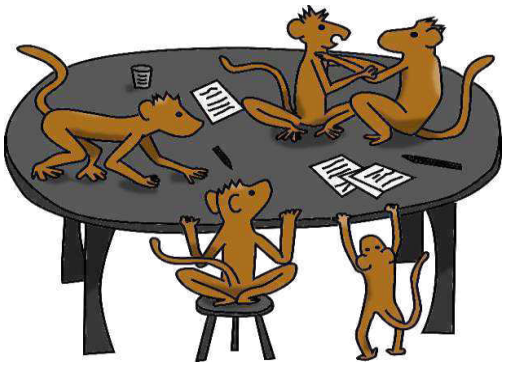
which did not resemble the calls produced by the top-ranking male of their community (Mitani & Gros-Louis, 1998). The societies of this species can be considered tolerant when compared to the range of social styles reported in macaques (de Waal, 1986; Silk et al., 2013; Rebout et al., 2017). As for the effect of kinship on acoustic similarity, the dependence of vocal similarity on the dominance system of the species lends support to other evidence indicating that patterns of communication covary with patterns of social organization (Dobson, 2012; Freeberg et al., 2012). Moreover, a stronger effect of kinship on vocal similarity in rhesus macaques, linked to a higher degree of closure of matrilines compared to Tonkean macaques, may explain that we did not find an effect of group membership in the former species. In other words, open social relationships would favor acoustic similarity at group scale in tolerant species, whereas similarity would rather occur between individuals belonging to same subgroups in more nepotistic species.

It has been suggested that vocal convergence promotes group cohesion and the identification of group members (Giles et al., 1991; Snowdon & Hausberger, 1997; Wilkinson & Boughman, 1998; Candiotti et al., 2012). It could also be that the variations observed between conspecifics are non-adaptive consequences of genetic divergence and/or individual learning abilities (Thierry, 1994). Differences between calls emitted by different categories of females did indeed remain subtle. The search for limited variations in behaviours and vocalizations often provides evidence of inter-group differences in non-human primates (e.g., Crockford et al., 2004; Tanaka et al., 2006; Nakagawa et al., 2015), which may prove to be a general phenomenon among primates.

Although no one disputes the fact that humans have far greater control over their vocal production apparatus, a certain degree of volitional control in vocal production has however been recently reported in some Old and New World monkeys and apes. For example, gibbons can be conditioned to vocalise on command (Koda et al., 2007), they voluntarily perform a precise tuning of frequencies when singing in a helium chamber (Koda et al., 2012), and orang-utans (*Pongo* sp.) can instantaneously match human-produced sounds as they are randomly modulated in pitch (Lameira et al., 2016). Some recent neurobiological studies suggested the existence in non-human primates of a cognitive neuronal network capable of taking control over a basic vocal motor network that produces largely innate vocal utterances but lacks the ability to learn or imitate new vocal signals (Hage et al., 2013; Ackermann et al., 2014; Hage, 2018). These studies also suggested the importance of auditory feedback – notably from family members – on this cognitive vocal motor control; they pointed to a possible role of audio-vocal networks and cortico-basal loops in experience-dependent modifications of the acoustic call structure during vocal development in non-human primates (Hage, 2018). However, it appears important to distinguish vocal flexibility in the production of innate vocalizations – as shown

in both monkeys and apes (Lemasson et al., 2011; Watson et al., 2015) – from vocal flexibility in the production of new vocalizations beyond the species innate repertoire – as found in apes only (Hopkins et al., 2007; Lameira et al., 2013). Belyk and Brown (2017) proposed an alternative scenario where voluntary control of the vocal apparatus and vocal production learning co-evolved with a progressive modification of brain morphology throughout the audiovisual system across primate orders. They suggested a neurophenotypic continuum from monkeys to great apes to humans. The issue is still debated. With regard to macaques, our findings support a more finely-tuned control than previously expected, and are in line with previous works showing that female Japanese macaques can modify the fundamental frequency pattern of their calls – namely duration and amplitude of frequency modulation – to attract attention from others (Koda, 2004), and are thus at least capable of controlling both their airflow and vocal fold oscillation in a limited but perceptible way.

The present results highlight the flexibility of vocal communication in primates like macaques and underline the influence of social style on this ability. The investigation should now be extended to other types of vocalizations in further groups and species to assess the generality of our conclusions, and must include playback experiments that aim to study the functional significance of the variation evidenced here.



CHAPTER 8
General discussion

In this work, I have developed a new methodology for studying complexity and applied it to test the social complexity hypothesis for communicative complexity in macaques. I will discuss the research perspectives it opens.

1. Issues and solutions in measuring complexity

As explained in the General introduction, there are many definitions of complexity. However, most of them are not satisfactory and lack a theoretical basis for measuring complexity. The same elements are often considered as indicators of complexity (e.g. number of individuals, number of call types). I myself have taken a different approach. To address complexity, one solution to the problem is to break it down into several dimensions. It was by referring to the structure and function of a system that I have recognized the multidimensional aspect of complexity. This has allowed me to develop a complementary approach at several levels. Thus, I have defined three levels of study of systems and therefore three levels at which complexity can be studied: diversity, flexibility, and combinability (Chapter 3). I acknowledged that each level can be studied in terms of structure and context (Chapter 5 & 6).

Following the decomposition of the complexity into three levels, I proposed a measure for each dimension. There is agreement that complex system are systems displaying a high degree of uncertainty (McDaniel and Driebe 2005; Schuster 2016). It was to quantify the levels of uncertainty within systems that I considered Shannon's information theory (Shannon 1948). The key concept of this theory, entropy, makes it possible to measure the uncertainty of a system. Therefore, I applied Shannon's formula for entropy as a basis for developing indices for each dimension of complexity (Chapter 3). It is also the entropy formula that allowed me to quantify the degree of gradation of a repertoire (Chapter 4 & 5), as well as the strength of the association between the acoustic structure of vocalizations and their context of emission (Chapter 6). Shannon's entropy is often used to quantify the diversity of a system. This thesis should demonstrate that it is possible to use this theory much more widely to address complexity.

Even if a mathematical quantification of complexity allows to rigorously quantify the complexity of a system, comparing complexity between different species or systems is not straightforward. I have therefore proposed a method for calculating complexity indices related to diversity, flexibility and combinability. This makes it possible to compare different systems that may not have the same number of discrete categories (Chapter 3). However, what happens when it is not possible to define discrete categories, as is the case for a graded system? To answer this question, I have developed a robust and objective method for comparing graded systems in terms of diversity and flexibility (Chapter 4). Although I have designed this method

to compare the vocal system of macaques (Chapter 5), it will also be useful to compare other communication systems (e.g. facial expression repertoires), and can be extended to fields other than behavioural studies, e.g. to investigate the cell structure of organs for example (Schaum et al. 2018).This method can also be applied beyond the comparative approach. This is an approach to consider in species where gradation between call types has so far severely limited the establishment of vocal repertoires (e.g. crows, *Corvus frugilegus*: (Roskaft and Espmark 1982; Mates et al. 2015). Finally, I have developed a complementary procedure to compare the strength of the link between the acoustic structure of vocalizations and their context of emission (Chapter 6). It allows to study this link in an objective and robust way, without relying on subjective categories. To my knowledge, this is the first method that proposes to quantify the degree of association between signal structure and context in a comparative approach.

I expect my index and methods to be applicable to different areas of study, going beyond animal communication and testing the social complexity hypothesis. There is still room for improvement since each dimension of complexity can be measured in multiple ways, with a greater number of variables. With regard to the testing of the social complexity hypothesis, my approach should raise awareness of the fact that concluding that the social or vocal system of a species is complex or not is a much less interesting question than concluding on what dimension this species is complex or not. There are multiple and distinct dimensions to consider and compare in order to fully understand complex systems.

2. Testing the social complexity hypothesis

I carried out a detailed analysis of the influence of the degree of social tolerance on vocal communication. I highlighted several differences between tolerant and intolerant macaque species. The vocal similarity of contact calls was not influenced by dominance relationships in (tolerant) Tonkean macaques as opposed to (intolerant) rhesus macaques (Chapter 7) and Japanese macaques (Lemasson et al. 2016). This revealed an effect of the social style on patterns of communications (see Dobson 2012; Freeberg et al. 2012a), consistent with the fact that intolerant macaques display strong power asymmetries between individuals compared to more tolerant macaques that are characterized by more relaxed dominance relationships. Tonkean and crested macaques, the more tolerant species, exhibited a higher degree of vocal diversity in an agonistic context compared to Japanese and rhesus macaques, the more intolerant species. Additionally, tolerant macaques showed a higher degree of gradation in their vocalizations for the agonistic and affiliative contexts (Chapter 5), and a lower degree of context specificity regarding call emission (Chapter 6). These results can be considered as a further sign of ambiguity in macaque vocal production and this can be understood in relation to their level of

social tolerance. The outcome of the social interactions of tolerant species such as Tonkean and crested macaques is not easily predictable from their dominance and kinship relationships, they have better skills than intolerant macaques in the social domain, and they often switch quickly from aggression to flight, protest or reconciliation for example (Thierry et al. 1994; Thierry 2000, 2007; Duboscq et al. 2014; Joly et al. 2017). What can be considered as ambiguity in communication can also be considered as richness.

Functionally, a richer and more subtle communication system provides the potential to express more nuanced meanings – resulting in a looser association between structure and context) (Chapter 6) – and may convey a wider range of emotions and intentions (Morton 1977; Freeberg et al. 2012a). Additionally, more richness in communication (Chapter 5 & 6) gives tolerant macaques the opportunity to manage uncertainty in their social interactions, as they characterized by a greater degree of freedom and a greater number of possible outcomes (Thierry 1990; Butovskaya 2004; Flack and de Waal 2004; Duboscq et al. 2017). That may have helped them to manage social conflicts and achieve high rates of conflict resolution (de Waal 1993; Petit and Thierry 1994; Thierry 2007; De Marco et al. 2014; Duboscq et al. 2014). Tolerant macaques appear less constrained than intolerant macaques in terms of hierarchical relations (Chapter 7). By also being less vocally constrained, tolerant macaques have a greater freedom of expression; they can emit specific comments on outgoing events (Chapter 6), where they express their emotional response while witnessing social interactions. This likely sustains the strong commitment to the behaviour of others displayed by Tonkean and crested macaques, and their frequent polyadic interactions (Petit and Thierry 1994, 2000; Petit et al. 2008; Palagi et al. 2014; Puga-Gonzalez et al. 2014). My results show that the degree of freedom at the social level is also found at the vocal level. This contributes to our understanding of the social styles of macaques, providing evidence of the role of structural constraints in the evolution of primate societies (Thierry 2007, 2013).

The primary objective of my thesis was to test the social complexity hypothesis for communicative complexity. I have shown that tolerant species have a higher degree of vocal diversity and flexibility. This correlates with a higher degree of uncertainty in their social interactions, and therefore with their higher level of social complexity. I have found a link between social complexity and two dimensions of vocal complexity, namely diversity and flexibility (Table 1). In terms of vocal diversity, tolerant species exhibited a higher number of groups of calls in the agonistic context compared to intolerant species (Chapter 5). In terms of vocal flexibility at the structure level, tolerant species exhibited a higher degree of gradation between groups of calls in the agonistic and affiliative contexts (chapter 5). In terms of vocal flexibility at the level of structure at the context level, tolerant macaques had a higher degree of freedom than their intolerant counterparts in the association between vocal structure and social context (Chapter 6). Studying the context specificity of calls as well as the degree of

differentiation in commenting calls, I found that Tolerant macaques use signals that are weakly dependent on context, which leaves a great deal of uncertainty in their vocal communication, but also a higher degree of freedom. Taken together (Chapter 5 & 6), these results show in tolerant macaques a more diverse and flexible vocal communication, offering a wider range of expression that could allow them to better manage the uncertainty of their social interactions. These results strongly support the social complexity hypothesis.

Table 1. Comparative results about the diversity and flexibility of vocal signalling in four species of macaque.

	Japanese macaques	rhesus macaques	Tonkean macaques	crested macaques
Diversity				
Structural diversity				
Mean number of group of calls				
• Agonistic context	2.53	2.51	3.57	3.42
• Affiliative context	2.03	3.29	3.95	4.19
• Neutral context	2.34	4.74	3.09	3.11
Flexibility				
Structural flexibility				
Degree of gradation in calls (MRE)[1]				
• Agonistic context	0.215	0.208	0.312	0.267
• Affiliative context	0.275	0.255	0.310	0.345
• Neutral context	0.295	0.304	0.250	0.286
Contextual flexibility				
Strength of structure context link (MRE)	0.473	0.304	0.250	0.286
Differentiation of commenting calls	NA[2]	-[3]	+	+

[1]MRE: mean relative entropy.
[2]NA: missing data.
[3]+ and - : respectively, significant and non-significant differences in acoustic structure between commenting calls and uncontextualized calls.

When testing the social complexity hypothesis, there are inevitably some confounding factors. To limit the factors of variations, species should ideally differ only in their degree of social complexity, and be phylogenetically close, live in the same environments, while having the same type of social organization. In this work, I studied species belonging to the same genus to make homologous comparisons. To date, there is no evidence of ecological influence on the variables related to social complexity (Ménard, 2004; Thierry, 2007) or vocal complexity (Chapter 5 & 6).

On the other hand, among the species I have compared, those that were more similar in terms of social complexity (intolerant and tolerant macaques) were also phylogenetically closer (the Japanese/rhesus pair and the Tonkean/crested pair). Therefore, are the highlighted effects a consequence of the co-evolution between vocal and social patterns as stated by the complexity hypothesis, or can they be a side-effect of phylogenetic relationships? Several results indicate that the differences in vocal complexity are not a mere outcome of historical evolutionary pathways. Indeed, the latter assumption posits that closely related species show generalized similarity in many patterns of vocal structure in all social contexts, and not just those related to vocal complexity. A phylogenetic correlation fails to explain why the two pairs of species differed in acoustic distances, nor why the contrasts were consistent in some contexts – agonistic context for vocal diversity, agonistic and affiliative contexts for vocal flexibility – and not in other contexts – affiliative and neutral contexts for vocal diversity, neutral context for vocal flexibility. On the contrary, the social complexity hypothesis can account for these contrasts. It explains that only the complexity variables, i.e. vocal diversity and flexibility, show significant differences between the Tonkean/crested and Japanese/rhesus pairs in the social context with the highest level of uncertainty (agonistic context), and that variations are less pronounced or absent in the other contexts (affiliative and neutral contexts).

To distinguish the respective influence of phylogeny and social complexity – as reflected in the level of social tolerance – a promising line of inquiry would be to study a fifth species that is phylogenetically close to some macaques, and at the same time close in the degree of social tolerance to others. The pigtailed macaques appear to be good candidates for such objectives. They belong to the *silenus-sylvanus* lineage and are therefore phylogenetically close to tolerant species such as Tonkean and crested macaques. However, pigtailed macaques are on grade 2 of the macaque social style scale (Thierry, 2007), which means that they belong to the intolerant side of macaques. Moreover, the pigtailed macaque seem close to intolerant macaques from the point of view of their vocal repertoire, particularly with the production of growls (Grimm, 1967). I would expect pigtailed macaques to display vocal signals of similar complexity to

Japanese and rhesus macaques, although they are closer phylogenetically to Tonkean and crested macaques.

The relationship between vocal and social complexity – and more generally between communication and social organization – may arise at both the proximate and the ultimate levels, and the social complexity hypothesis includes both. As the current work is based on interspecific comparisons, its results can be interpreted in the light of the constraints having occurred during the evolutionary process, but this does not rule out the intervention of proximate mechanisms at the scale of interindividual interactions. It should also be stressed that these results are correlative and cannot be used as evidence of causal effects (McComb & Semple, 2005). While it is generally assumed that the emergence of complex social systems leads to greater vocal complexity (Blumstein & Armitage, 1997; Gustison, le Roux, & Bergman, 2012; McComb & Semple, 2005; Pollard & Blumstein, 2012), this should not be taken for granted (Kappeler, 2019; Semple, McComb, Alberts, & Altmann, 2002). There is currently no data available to know whether social complexity precedes communication complexity or vice versa (Peckre et al. 2019). A high level of social complexity in a species may require the development of elaborate communicative skills, but elaborate communicative skills may allow as well the emergence of complex social relationships and interactions. These two process are not mutually exclusive. The occurrence a co-evolution between social and communicative complexity is likely, which would induce a a positive feedback loop.

To investigate the issue at a proximate level, a cross-fostering procedure would be advisable, involving the adoption of an infant from of tolerant species by a mother from an intolerant species, and vice versa. This would make it possible to test whether the complexity of vocal signalling in these individuals would be modified by their social environment. It should be added however that such experiments would not only raise technical difficulties and questions about the accuracy of communications between two different species, but also serious ethical problems since the future of the adopted individuals would be compromised.

At the evolutionary level, there is no evidence that social complexity, as measured by the number of individuals in a group – admittedly a questionable measure – has evolved in a linear way. Phylogenetic analyses indicate that the social organization of primates has shifted from solitary foraging individuals to multimale/multifemale groups during the evolutionary history of the order, and that that pair-living and single-male social systems are secondarily derived from the multimale/multifemale system (Shultz et al., 2011). We may find a second instance of non-linear historical process can be found if we consider the 4-grade scale of macaques (Thierry, 2000), while measuring social complexity in macaques using the degree of uncertainty, i.e. the degree of social tolerance. Phylogenetic analyses have revealed that grade 3 is the most ancestral state in the genus, grade 4 (e.g. Tonkean & crested macaques) is a derived

but ancient state, and grade 1 (e.g. Japanese & rhesus macaques) is the most recent state (Thierry, Iwaniuk, & Pellis, 2000). This last finding means that, for some unknown reason, macaques have evolved from a higher degree to a lower degree of social complexity. It is all the more interesting to discover a link between social and vocal complexity. The social complexity hypothesis is a functional hypothesis and remains valid regardless of the direction of social evolution.

3. Perspectives

Communication depends not only on the caller, but also on the listener. I found that tolerant macaques have more nuanced signals than more intolerant macaques, with a higher level of gradation in their vocal repertoire (Article 3), and a weaker association between the acoustic structure of the calls and their context of emission (Article 4). These two characteristics give *a priori* callers the possibility to express a wider range of meanings. However, it is the receiver who assigns meaning by inferring the content of the information (Fischer 2013), so it would now be necessary to study how individuals perceive call variations. I found that contrasts in terms of vocal diversity and flexibility were more pronounced in the agonistic context (Article 3). Several authors have conducted playback experiments in which the vocalizations tested were agonistic calls such as screams. This has shown that chimpanzees can distinguish between different call variants (Katie Elizabeth Slocombe, Townsend, & Zuberbühler, 2009), and that rhesus macaques are able to distinguish noisy from non-noisy ones (Fugate, Gouzoules, & Nygaard, 2008). Other authors suggest that although gradation occurs in the primate vocal repertoire, individuals may perceive calls discreetly (Hammerschmidt & Fischer, 1998; Marler, 1976; Katie E Slocombe & Zuberbühler, 2007, Fischer, Metz, Cheney & Seyfarth, 2001; Hauser, 1996), but little is yet known about the perception of graded repertoires in many species. Playback experiments could be performed in macaques to test the effect of different levels of call gradation on the receiver's response. To such aims, it would be interesting to use the so-called 'intermediate calls' identified thanks to analyses as belonging to several clusters, and investigate the ability of listeners to respond differently to the different categories of calls.

While this thesis focused on vocal communication, the comparison between tolerant and intolerant macaques could be extended to other communication modalities. Dobson (2012) showed that more tolerant macaques tend to have a greater repertoire of facial displays than less tolerant ones. However, his study was limited to the number of displays, based on scientific literature. In recent years, the Facial Action Coding System (FACS) has been developed for macaques (Julle-Danière et al. 2015; Micheletta et al. 2015), which allows detailed

measurement of facial muscle movements. The methods developed here to analyse diversity and flexibility could be applied to the study of facial communications using FACS. Moreover, primates and macaques in particular communicate in a multimodal way (Liebal et al. 2012; Micheletta et al. 2013), and this ability may be related to complexity. A high degree of uncertainty can be expected if individuals use a large number of modalities (diversity), if they use these modalities rather independently from context (flexibility), and if they use many different combinations of modalities (combinability).

It should be kept in mind that I have tested the social complexity hypothesis at the level of social interactions. However, individuals regularly interact with each other throughout their lives, creating a historical context (Smith 1965). It makes sense to also consider uncertainty at the levels of social relationships or social networks. A possible approach to do this would be to consider the calls emitted during vocal exchanges. For example, if there is a strong influence of dominance relationships, the vocal expression of a low-ranking individual could be more constrained when exchanging calls with a high-ranking partner than with a partner similar in rank. Because constraints in vocal expression mean less vocal complexity, I expect the degree of complexity of vocalizations to vary with the social relationship between caller and listener to a greater extent in intolerant than in tolerant species. In Article 5, I tested the effect of social complexity on vocal similarity in terms of relationships, but this was not strictly related to vocal complexity. There should more uncertainty if there is a greater degree of freedom between acoustic structure and kinship or dominance relationships. The method used in in Article 4 in particular could be adapted to test the strength of the association between the acoustic structure and social relationships.

The identification of diversity and flexibility was a necessary step before addressing the third dimension of complexity, i.e. combinability (Article 1). Although I have not yet compared the previously tolerant and intolerant macaques in terms of their combinatorial abilities, some preliminary elements are suggestive. Article 1 suggests that there is a certain gradation in the dimensions of complexity; Tonkean and rhesus macaques were indeed different in social diversity, slightly more different in social flexibility, and even more different in social combinability. The same trends can be seen in vocal diversity and flexibility (Articles 2 & 3), and I expect the existence of especially strong contrasts in vocal combinability. Tolerant species may emit longer sequences with more diverse types of calls than intolerant species. I also expect that the diversity of transitions between calls within a sequence will be greater in tolerant than in intolerant species. It seems that Tonkean and crested macaques are able to move quickly from one call to a different one in a kind of continuum, for example from bark to scream through chuckles in the agonistic context. With regard to the affiliative context, they can combine several affiliative calls and growls in different proportions. Similar occurrences seem much less

frequent in intolerant macaques. Such observations have still to be confirmed through quantitative analyses. The richness of the sequences can be approximated by entropy calculations or Markov chain analyses, particularly suitable for the analysis of complexity in vocal sequences (Kershenbaum et al. 2014, 2016). However, this type of approach requires a discrete system, i.e. with vocalizations identified and labelled before analysis, which is difficult when the system is graded. A possible solution to this problem is to define broad categories rather than trying to distinguish between subtypes; however, it might still be difficult to make the difference between close call categories such as 'low coos' and 'soft grunts' for example. Another solution would be to let a cluster algorithm identify categories, and label calls in sequences accordingly.

Finally, in addition to sequences analyses to compare species in terms of vocal combinability, a preliminary study of non-linear phenomena in vocalizations suggested a potential ability of macaques to combine two calls in the same vocal continuity. Non-linear phenomena in animal calls are common, but they are traditionally overlooked (Fitch et al. 2002). The presence of non-linear phenomena has been demonstrated in non-human primates (Fitch et al. 2002; Riede et al. 2004; Rice et al. 2011). Deterministic chaos in screams have been found in Japanese macaques (Tokuda et al. 2002), and frequency jumps have also been found in common chimpanzees (Riede et al. 2004). Fitch and colleagues (2002) argue that non-linear phenomena allow individuals to generate particularly complex and unpredictable vocalizations. My preliminary results suggest that tolerant macaques have a higher proportion of non-linear phenomena in their vocalizations. In addition to rate differences, non-linear phenomena do not seem to in the same place in the calls of tolerant and intolerant species. In intolerant macaques, sub-harmonics seem to be preferentially located in the middle of the calls. These sub-harmonics within calls could underline an emotional response because they appear mostly in food calls and screams. On the contrary, in tolerant macaques, sub-harmonics seem to be more frequent at the end of the calls, and are found in 'coos', which gives these calls the appearance of two calls. I intend to explore this issue further. I expect tolerant macaques to be able to concatenate two calls almost continuously and to a greater extent than intolerant macaques.

4. Conclusion

In this thesis, I developed several tools to measure and compare the complexity of systems. I took into account the multidimensional nature of complexity by defining three components: diversity, flexibility and combinability. I then developed quantitative indices to compare four species of macaque. I have tested the hypothesis of social complexity on two dimensions, diversity and flexibility. This has shown that tolerant macaques display more complex vocal communication than more intolerant macaques in terms of structural diversity, structural flexibility and contextual flexibility. Their vocal signals also appear richer and more flexible than those of their more intolerant counterparts. Such interspecific variations are related to difference in the degree of uncertainty of social interactions. These results support the social complexity hypothesis for communicative complexity. A main task in the immediate future will be to address macaque contrasts through their abilities in terms of vocal combinability.

BIBLIOGRAPHY

Abdi H, Williams LJ (2010) Principal component analysis. Wiley Interdisc Rev Comput Stat 2:433–459.

Ackermann H, Hage SR**,** Ziegler W (2014) Phylogenetic reorganization of the basal ganglia: a necessary, but not the only, bridge over a primate Rubicon of acoustic communication. Behav Brain Sci 37:577–604.

Adams MJ, Majolo B, Ostner J, Schülke O, De Marco A, Thierry B, Engelhardt A, Widdig A, Gerald MS & Weiss A (2015) Personality structure and social style in macaques. J Pers Soc Psychol 109:338–353.

Albert I, Ancelet S, David O, Denis JB, Makowski D, Parent E, Rau A, Soubeyrand S (2015) Initiation à la statistique bayésienne. Ellipses, Paris.

Alberts B, Hopkin K, Johnson AD, Morgan D, Raff M, Roberts K, Walter P (2019) Essential cell biology, 5th ed. Norton, New York, NY.

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267.

Altmann SA (1962) A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Ann N Y Acad Sci 102:338–435.

Anderson C, Keltner D, John OP (2003) Emotional convergence between people over time. J Pers Soc Psychol 84:1054–1068.

Antonovics J, van Tienderen PH (1991) Ontoecogenophyloconstraints? The chaos of constraint terminology. Trends Ecol Evol 6:166–168.

Arlet ME, Jubin R, Masataka N, Lemasson A (2015) Grooming-at-a-distance by exchanging calls in non-human primates. Biol Lett 11:20150711.

Arnold K, Zuberbühler K (2006) Language evolution: semantic combinations in primate calls. Nature 441:303.

Arnold K, Zuberbühler K (2008) Meaningful call combinations in a non-human primate. Curr Biol 18:202–203.

Arnold K, Zuberbühler K (2013) Female putty-nosed monkeys use experimentally altered contextual information to disambiguate the cause of male alarm calls. Plos One 8:2–8.

Arriaga G, Zhou EP, Jarvis ED (2012) Of mice, birds, and men: the mouse ultrasonic song system has some features similar to humans and song-learning birds. Plos One 7:e46610.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654.

Balasubramaniam KN, Beisner BA, Berman CM, De Marco A, Duboscq J, Koirala S, Majolo B, MacIntosh AJJ, McFarland R, Molesti S, Ogawa H, Petit O, Schino G, Sosa S, Sueur C, Thierry B, de Waal FBM, McCowan BJ (20187) The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. Am J Primatol 80:e227271.

Balasubramaniam KN, Dittmar K, Berman CM, Butovskaya M, Cooper MA, Majolo B, Ogawa H, Schino G, Thierry B, de Waal FBM (2012) Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. Anim Behav 83:1207–1218.

Banfield JD, Raftery AE (1993) Model-based Gaussian and non-Gaussian clustering. Int Biometric Soc 49:803–821.

Barton K (2016) MuMIn: multi-model inference. R Package version 1.15.6. https://CRAN.R-project.org/package=MunMn

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J. Stat. Soft 67:1–48.

Becker AE, Kleinman A (2000) Anthropology and psychiatry. In: BJ Sadock & VA Sadock (eds), Kaplan & Sadock's comprehensive textbook of psychiatry, 7th ed. Lippincott Williams & Wilkins, Philadelphia, PA, pp 463–476.

Bell G, Mooers AO (1997) Size and complexity among multicellular organisms. Biol J Lin Soc 60:345–363.

Belyk M, Brown S (2017) The origins of the vocal brain in humans. Neurosci Biobehav Rev 77:177–193.

Belzung C, Anderson JR (1986) Social rank and responses to feeding competition in rhesus monkeys. Behav Proc 12:307–316.

Ben-Hur A, Guyon I (2003) Detecting stable clusters using principal component analysis. Functional Genom 224:159–182.

Bergman TJ, Beehner JC (2015) Measuring social complexity. Anim Behav 103:203–209.

Berman CM, Thierry B (2010) Variation in kin bias: species differences and time constraints in macaques. Behaviour 147:1863–1887.

Berthet M, Neumann C, Mesbahi G, Cäsar C, Zuberbühler K (2018) Contextual encoding in titi monkey alarm call sequences. Behav Ecol Sociobiol 72:1–11.

Biben M, Symmes D (1986) Play vocalizations of squirrel monkeys (*Saimiri sciureus*). Folia Primatol 46:173–182.

Blount BG (1985) "Girney" vocalizations among Japanese macaque females: context and function. Primates 26:424–435.

Blumstein DT, Armitage KB (1997) Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. Am Nat 150:179–200.

Boesch C (2002) Cooperative hunting roles among Taï chimpanzees. Hum Nat 13:27–46.

Borst A, Theunissen FE (1999) Information theory and neural coding. Nat Neurosci 2: 947–957.

Bouchet H, Blois-Heulin C, Lemasson A (2013a) Social complexity parallels vocal complexity: a comparison of three non-human primate species. Front Psychol 4:1–15.

Bouchet H, Blois-Heulin C, Pellier AS (2012) Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). J Comp Psychol 126:45–56.

Bouchet H, Koda H, Lemasson A (2017) Age-dependent change in attention paid to vocal exchange rules in Japanese macaques. Anim Behav 129:81–92.

Bouchet H, Laporte M, Candiotti A, Lemasson A (2013b) Flexibilité vocale sous influences sociales chez les primates non-humains. Rev Primatol 5.

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland, MA.

Briefer EF (2012) Vocal expression of emotions in mammals: mechanisms of production and evidence. J Zool 288:1–20.

Briefer EF, McElligott AG (2012) Social effects on vocal ontogeny in an ungulate, the goat, *Capra hircus*. Anim. Behav 83:991–1000.

Briskie J V, Martin PR, Martin TE (1999) Nest predation and the evolution of nestling begging calls. Proc R Soc B 266:2153–2159.

Brooks DR, McLennan DA (2013) The nature of diversity. An evolutionary voyage of discovery. University of Chicago Press, Chicago, IL.

Brumm H, Kipper S, Riechelmann C, Todt D (2005) Do Barbary macaques "comment" on what they see? A first report on vocalizations accompanying interactions of third parties. Primates 46:141–144.

Bshary R, Noë R (1997) Red colobus and Diana monkeys provide mutual protection against predators. Anim Behav 54:1461–1474.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York, NY.

Butovskaya M (2004) Social space and degree of freedom. In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 4182–185.

Butts CT (2001) The complexity of social networks: theoretical and empirical findings. Soc Networks 23:31–71.

Candiotti A, Zuberbühler K, Lemasson A (2012) Convergence and divergence in Diana monkey vocalizations. Biol Lett 8:382–385.

Carneiro RL (2003) Evolutionism in cultural anthropology: a critical history. Westview Press, Boulder, CO.

Carroll SB (2001) Chance and necessity: the evolution of morphological complexity and diversity. Nature 409: 1102–1109.

Chaitin GJ (2003) Randomness and mathematical proof. In: NH Gregersen (ed), From complexity to life: on the emergence of life and meaning (ed). Oxford University Press, Oxford, pp 19–33.

Chauvin C, Thierry B (2005) Tonkean macaques orient their food search from olfactory cues conveyed by conspecifics. Ethology 111:301–310.

Chen HC, Kaplan G, Rogers LJ (2009) Contact calls of common marmosets (*Callithrix jacchus*): iInfluence of age of caller on antiphonal calling and other vocal responses. Am J Primatol 71:165–170.

Cheney DL, Seyfarth RM (1980) Vocal recognition in free-ranging vervet monkeys. Anim Behav 28:362–367.

Cheney DL, Seyfarth RM (2018) Flexible usage and social function in primate vocalizations. Proc Natl Acad Sci USA 115:1974–1979.

Cherry C (1955) Communication theory—and human behaviour. In: BI Evans (ed), Studies in communication. Martin Secker & Warburg, London, pp 45–67.

Chu D, Strand R, Fjelland R (2003) Theories of complexity. Common denominators of complex systems. Complexity 8:19–30.

Ciani F, Dall'Olio S, Stanyon R, Palagi E (2012) Social tolerance and adult play in macaque societies: a comparison with different human cultures. Anim Behav 84:1313–1322.

Clay Z, Zuberbühler K (2009) Food-associated calling sequences in bonobos. Anim Behav 77:1387–1396.

Cleveland J, Snowdon CT (1982) The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). Z Tierpsychol 58:231–270.

Cleveland J, Snowdon CT (1984) Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus oedipus oedipus*). Anim Behav 32:432–444.

Clutton-Brock T, Janson C (2012) Primate socioecology at the crossroads: past, present, and future. Evol Anthropol 21:136–150.

Cochet H, Byrne RW (2014) Complexity in animal behaviour: towards common ground. Acta Ethol 18:237–241.

Collins NM, Sayer JA, Whitmore TC (1991) The conservation atlas of tropical forests: Asia and the Pacific. Simon & Schuster, New York, NY.

Connor RC (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Phil Trans R Soc B 362:587–602.

Corning PA, Szathmáry E (2015) "Synergistic selection": a Darwinian frame for the evolution of complexity. J Theor Biol 371:45–58.

Cowlishaw G, Dunbar RIM (1991) Dominance rank and mating success in male primates. Anim Behav 41:1045–1056.

Crockford C, Boesch C (2003) Context-specific calls in wild chimpanzees, *Pan troglodytes* verus: analysis of barks. Anim Behav 66:115–125.

Crockford C, Herbinger I, Vigilant L, Boesch C (2004) Wild chimpanzees produce group-specific calls: a case for vocal learning? Ethology 243: 221–243.

Danchin E, Giraldeau LA, Cézilly F (2008) Behavioural ecology. Oxford University Press, Oxford.

Darwin C (1872) The expression of the emotions in man and animals, John Murray, London.

Davidson SM, Wilkinson GS (2002) Geographic and individual variation in vocalizations by male *Saccopteryx bilineata* (*Chiroptera*: *Emballonuridae*). J Mammal 83:526–535.

Davies NB, Krebs JR, Stuart AW (2012) An introduction to behavioural ecology. Wiley-Blackwell, Oxford.

de la Torre S, Snowdon CT (2009) Dialects in pygmy marmosets? Population variation in call structure. Am J Primatol 71:333–342.

De Marco A, Rebout N, Massiot E, Sanna A, Sterck EHM, Langermans JAM, Cozzolino R, Thierry B, Lemasson A (2019) Differential patterns of vocal similarity in tolerant and intolerant macaques. Behaviour 156:1–25.

De Marco A, Sanna A, Cozzolino R, Thierry B (2014) The function of greetings in male Tonkean macaques. Am J Primatol 76:989–998.

de Vries H, Netto WJ, Hanegraaf PLH (1993) Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour 125:157–175.

de Waal FBM (1986) The integration of dominance and social bonding in primates. Q Rev Biol. 61:459–479.

de Waal FBM (1993) Reconciliation among primates: a review of empirical evidence and unresolved issues. In: Mason WA, Mendoza SP (eds), Primate social conflict. State University of New York Press, Albany, NY, pp 111–144.

de Waal FBM, Luttrell LM (1985) The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. Am J Primatol 9:73–85.

Deecke VB, Janik VM (2006) Automated categorization of bioacoustic signals: avoiding perceptual pitfalls. J Acoust Soc Am 119:645–653.

Delson E (1980) Fossil macaques, phyletic relationships and a scenario of deployment. In: DG Lindburg (ed), The macaques: studies in ecology, behavior and evolution. Van Nostrand Rheinhold, New York, NY, pp 10–30.

Delson E, Rosenberger AL (1980) Phyletic perspectives on Platyrrhine origins and anthropoid relationships. In: RL Ciochon (ed), Evolutionary biology of the New World monkeys and continental drift. Plenum Press, New York, NY, pp 445–458

Demaria C, Thierry B (2001) A comparative study of reconciliation in rhesus and Tonkean macaques. Behaviour 138:397–410.

Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci USA 91:9941–9945.

Dittus WPJ (1984) Toque macaque food calls: semantic communication concerning food distribution in the environment. Anim Behav 32:471–477.

Dobson SD (2012) Coevolution of facial expression and social tolerance in macaques. Am J Primatol 74:229–235.

Doxiadis GGM, de Groot N, Otting N, de Vos-Rouweler AJM, Bolijn MJ, Heijmans CMC, de Groot NG, van der Wiel MKH, Remarque EJ, Vangenot C, Nunes JM, Sanchez-Mazas A, Bontrop RE (2013) Haplotype diversity generated by ancient recombination-like events in the MHC of Indian rhesus macaques. Immunogenetics 65:569–584.

Dressnandt J, Jürgens U (1992) Brain stimulation-induced changes of phonation in the squirrel monkey. Exp Brain Res 89:549–559.

Duboscq J, Agil M, Engelhardt A, Thierry B (2014) The function of postconflict interactions: new prospects from the study of a tolerant species of primate. Anim Behav 87:107–120.

Duboscq J, Micheletta J, Agil M, Hodges K,Thierry B, Engelhardt A (2013) Social tolerance in wild female crested macaques (*Macaca nigra*) in Tangkoko-Batuangus Nnature Rreserve, Sulawesi, Indonesia. Am J Primatol 75:361–375.

Duboscq J, Neumann C, Agil M, Perwitasari-Farajallah D, Thierry B, Engelhardt A (2017) Degrees of freedom in social bonds of crested macaque females. Anim Behav 123:411–426.

Duboscq J, Romano V, Sueur C, MacIntosh AJ (2016) Network centrality and seasonality interact to predict lice load in a social primate. Sci Rep 6:22095.

Dunbar RIM (1995) Neocortex size and group size in primates: a test of the hypothesis. J Hum Evol 28:287–296.

Dunbar RIM (2012) Bridging the bonding gap: the transition from primates to humans. Phil Trans R Soc B 367:1837–1846.

Eagle N, Macy M, Claxton R (2010) Network diversity and economic development. Science 328:1029–1031.

Edwin CJ, Chopra SRK (1984) Group characteristics of *Macaca mulatta* inhabiting submontane and montane forests of the Indian subcontinent: a comparative review. In: ML Roonwal, SM Mohnot, NS Rathore (eds), Current primate researches. Jodhpur University, Jodhpur, pp 307–313.

Emlen ST, Oring LW (2007) Evolution of mating systems. Science 1977:215–223.

Evans CS (1997) Referential signals. In: DH Owings, MD Beecher, NS Thompson (eds), Perspectives in ethology, Vol 12: Communication. Plenum Press, New York, NY, pp 99–143.

Everitt BS (2014) Finite mixture distributions. Wiley Statsref: Statistics Reference Online.

Everitt BS, Landau S (1998) The use of multivariate statistical methods in psychiatry. Stat Methods Med Res 7:253–277.

Everitt BS, Landau S, Leese M, Stahl D (2011) Cluster analysis, 5th ed. Wiley, Hoboken, MA.

Ey E, Pfefferle D, Fischer J (2007) Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. Primates 48:253–267.

Fedigan LM (1976) A study of roles in the Arashiyama West troop of Japanese monkeys (*Macaca fuscata).* Karger, Basel.

Fedurek P, Schel AM, Slocombe KE (2013) The acoustic structure of chimpanzee pant-hooting facilitates chorusing. Behav Ecol Sociobiol 67:1781–1789.

Feekes F (1982) Song mimesis within colonies of *Cacicus c. cela* (*Icteridae*, *Aves*). A colonial password? Z Tierpsychol 58:119–152.

FeldmanHall O, Shenhav A (2019) Resolving uncertainty in a social world. Nat Hum Behav 3:426–435.

Feng W, Bailey RM (2018) Unifying relationships between complexity and stability in mutualistic ecological communities. J Theor Biol 429:100–126.

Ferguson-Gow H, Sumner S, Bourke AFG, Jones KE (2014) Colony size predicts division of labour in attine ants. Proc R So B 281:20141411.

Fichtel C, Hammerschmidt K (2002) Responses of redfronted lemurs to experimentally modified alarm calls: evidence for urgency-based changes in call structure. Ethology 108:763–777.

Fischer J (2013) Information, inference and meaning in primate vocal behaviour. In: UE Stegmann (ed), Animal communication theory: information and influence. Cambridge University Press, Cambridge, pp 297–318.

Fischer J, Farnworth MS, Sennhenn-Reulen H, Hammerschmidt K (2017a) Quantifying social complexity. Anim Behav 130:57–66.

Fischer J, Hammerschmidt K, Todt D (1998) Local variation in Barbary macaque shrill barks. Anim Behav 56:623–629.

Fischer J, Price T (2017) Meaning, intention, and inference in primate vocal communication. Neurosci Biobehav Rev 82:22–31.

Fischer J, Wadewitz P, Hammerschmidt K (2017b) Structural variability and communicative complexity in acoustic communication. Anim Behav 134:229–237.

Fitch WT, de Boer B, Mathur N, Ghazanfar AA (2016) Monkey vocal tracts are speech-ready. Sci Adv 2:e1600723.

Fitch WT, Hauser MD (1995) Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on "honest" advertisement. Am J Primatol 37:191–219.

Fitch WT, Neubauer J, Herzel H (2002) Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. Anim Behav 63:407–418.

Flack JC, de Waal FBM (2004) Dominance style, social power, and conflict management: a conceptual framework. In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 157–182.

Fooden J (1980) Classification and distribution of living macaques (*Macaca* Lalecépède). In: DG Lindburg, The macaques: studies in ecology, behaviour and evolution. Van Nostrand Rheinold, New York, NY, pp 1–8.

Fox J (2003) Effect displays in R for Generalised Linear Models. J Stat Soft 8:1–27.

Freeberg TM (2006a) Social complexity can drive vocal complexity: group size influences vocal information in Carolina chickadees. Psychol Sci 17:557–561.

Freeberg TM (2006b) Social complexity can drive vocal complexity. Psychol Sci 17:557–561.

Freeberg TM, Dunbar RIM, Ord TJ (2012a) Social complexity as a proximate and ultimate factor in communicative complexity. Phil Trans R Soc B 367:1785–801.

Freeberg TM, Ord TJ, Dunbar RIM (2012b) The social network and communicative complexity: preface to theme issue. Phil Trans R Soc B 367:1782–1784.

Fuentes A (2007) Social organization: social systems and the complexities in understanding the evolution of primate behavior. In: CJ Campbell CJ, A Fuentes A, K MacKkinnon K, M Panger, SK Bearder (eds), Primates in perspective. Oxford University Press, Oxford, pp 609–621.

Fugate JMB, Gouzoules H, Nygaard LC (2008) Recognition of rhesus macaque (*Macaca mulatta*) noisy screams: evidence from conspecifics and human listeners. Am J Primatol 70:594–604.

Fukushima M, Doyle AM, Mullarkey MP, Mishkin M, Averbeck BB (2015) Distributed acoustic cues for caller identity in macaque vocalization. R Soc Open Sci 2:150432.

Gautier JP (1988) Interspecific affinities among guenons as deduced from vocalizations. In: A Gautier-Hion, F Bourlière, JP Gautier, J Kingdon (eds), A primate radation: evolutionary biology of the African guenons. Cambridge University Press, Cambdrige, pp 194–226.

Geissmann T (1984) Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pileatus* x *H. lar*). Folia Primatol 42: 216–235.

Geissmann T (2002) Duet-splitting and the evolution of gibbon songs. Biol Rev 77:57–76.

Giles H, Coupland N, Coupland J (1991) Accommodation theory: communication, context, and consequence. In: H Giles, N Coupland, J Coupland (eds), Context of accommodation: developments in sociolinguistics. Cambridge University Press, Cambridge, pp: 1–68.

Goeffrey M, Peel D (2000) Finite mixture models. John Wiley, Hoboken,.

Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc B 205:581–598.

Gouzoules H, Gouzoules S (1989) Design-features and developemental modification of pigtail macaque, *Mmacaca nemestrina*, agonistic screams. Anim Behav 37:383–401.

Gouzoules H, Gouzoules S (1990a) Body size effects on the acoustic structure of pigtail macaque (*Macaca nemestrina*) screams. Ethology 85:324–334.

Gouzoules H, Gouzoules S (1990b) Matrilineal signatures in the recruitment screams of pigtail macaques, *Macaca nemestrina*. Behaviour 115:327–347.

Gouzoules H, Gouzoules S (2000) Agonistic screams differ among four species of macaques: the significance of motivation-structural rules. Anim Behav 59:501–512.

Gouzoules H, Gouzoules S, Tomaszycki M (1998) Agonistic screams and the classification of dominance relationships: are monkeys fuzzy logicians? Anim Behav 55:51–60.

Gouzoules S, Gouzoules H, Marler P (1984) Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. Anim Behav 32:182–193.

Green SM (1975a) Variation of vocal pattern with social situation in the Japanese monkey *(Macaca fuscata*): a field study. In: LA Rosenblum (ed), Primate behavior: developments in field and laboratory research, Vol. 4. Academic Press, New York, NY, pp 304–314.

Green SM (1975b) Dialects in Japanese monkeys: vocal learning and cultural transmission of locale-specific vocal behavior ? Z Tierpsychol 38:304–314.

Gregory SW, Webster S (1996) A nonverbal signal in voices of interview partners effectively predicts communication accommodation and social status perceptions. J Pers Soc Psychol 70:1231–1240.

Gregory TR (2001) Coincidence, coevolution, or causation? DNA content, cell size, and the C-value enigma. Biol Rev 76:65–101.

Gruber T, Grandjean D (2017) A comparative neurological approach to the decoding of emotional expressions in primate vocalizations. Neurosci Biobehav Rev 73:182–190.

Gustison ML, Bergman TJ (2016) Vocal complexity influences female responses to gelada male calls. Sci Rep 6:19680.

Gustison ML, le Roux A, Bergman TJ (2012) Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates. Phil Trans R Soc B 367:1847–59.

Gustison ML, Semple S, Ferreri-Cancho R, Bergman TJ (2016) Linguistic law. Proc Natl Acad Sci USA 113:E2750–E2758.

Gustison ML, Townsend SW (2015) A survey of the context and structure of high- and low-amplitude calls in mammals. Anim Behav 105:281–288.

Hage SR (2018) Dual neural network model of speech and language evolution: new insights on flexibility of vocal production systems and involvement of frontal cortex. Curr Opin Behav Sci 2:80–87.

Hage SR, Gavrilov N, Nieder A (2013) Cognitive control of distinct vocalizations in rhesus monkeys. J Cogn Neurosci 25:1692–1701.

Hage SR, Gavrilov N, Nieder A (2016) Developmental changes of cognitive vocal control in monkeys. J Exp Biol 219:1744–1749.

Hammerschmidt K, Fischer J (1998) The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. Ethology 104:203–216.

Hammerschmidt K, Fischer J (2008) Constraints in primate vocal production. In: DK Oller, U Griebel (eds), Evolution of communicative flexibility: complexity, creativity, and adaptability in human and animal communication. TMIT Press, Cambridge, MA, pp 92–119.

Hauser MD (1996) The evolution of communication. MIT Press, Cambridge, MA.

Hauser MD, Marler P (1993) Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. Behav Ecol 4:194–205.

Hedwig D, Mundry R, Robbins MM, Boesch C (2014) Contextual correlates of syntactic variation in mountain and western gorilla close-distance vocalizations: indications for lexical or phonological syntax? Anim Cogn 18:423–435.

Hennig C, Meila M, Murtagh F, Rocci R (2016) Handbook of cluster analysis. CRC Press, Boca Raton, FL.

Herrenschmidt N (1977) Semi-free breeding of tropical Celebes macaques (*Macaca tonkeana*) in continental European climate. J Med Primatol 6:58–65.

Hervé M (2017) RVAideMemoire: diverse basic statistical and graphical functions. R package version 0.9-65. https://CRAN.R-project.org/package=RVAideMemoire

Hidalgo CA, Hausmann R (2009) The building blocks of economic complexity. Proc Natl Acad Sci USA 106:10570–10575.

Hinde RA (1976) Interactions, relationships and social structure. Man 11:1–17.

Hinde RA, Rowell TE (1962) Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). Proc Zool Soc Lond 138:1–21.

Hodun A, Snowdon CT, Soini P (1981) Subspecific variation in the long calls of the tamarin, *Saguinus fuscicollis*. Z Tierpsychol 57:97–110.

Hoelzer G, Melnick DJ (1996) Evolutionary relationships of the macaques. In: J Fa, D Lindburg (eds), Evolution and ecology of macaque societies. Cambridge University Press, Cambridge, pp 3–19.

Hopkins WD, Taglialatela J, Leavens DA (2007) Chimpanzees differentially produce novel vocalizations to capture the attention of a human. Anim. Behav 11:281–286.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50: 346–363.

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40.

Humphrey NK (1976) The social function of intellect. In: PPG Bateson, RA Hinde (eds), Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317.

Hurford JR (2011) The origins of grammar: language in the light of evolution II. Oxford University Press, Oxford.

Janik VM (2014) Cetacean vocal learning and communication. Curr Opin Neurobiol 28: 60–65.

Jolliffe IT (2002) Principal component analysis, 2nd ed. Springer, New York.

Jolly A (1966) Lemur social behavior and primate intelligence. Science 153:501–506.

Joly M, Micheletta J, De Marco A, Langermans JA, Sterck EH, Waller BM (2017) Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. Proc R Soc B, 284:20162738.

Julle-Danière É, Micheletta J, Whitehouse J, Joly M, Gass C, Burrows AM, Waller BM (2015) MaqFACS (Macaque Facial Action Coding System) can be used to document facial movements in Barbary macaques (*Macaca sylvanus*). PeerJ 3:e1248.

Kappeler PM (2019a) Social complexity: patterns, processes, and evolution. Behav Ecol Sociobiol 73:5.

Kappeler PM (2019b) A framework for studying social complexity. Behav Ecol Sociobiol 73:13.

Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740.

Kassambara A (2017) Practical guide to principal component methods in R: multivariate analysis book. CreateSpace Independent Publishing Platform.

Katsu N, Nakamichi M, Yamada K (2016) Function of grunts, girneys and coo calls of Japanese macaques (*Macaca fuscata*) in relation to call usage, age and dominance relationships. Behaviour 153:125–142.

Katsu N, Yamada K, Nakamichi M (2017) Vocalizations during post-conflict affiliations from victims toward aggressors based on uncertainty in Japanese macaques. Plos One 12:1–15.

Kauffman SA (1993) The origins of order: self-organization and selection in evolution. Oxford University Press, New York, NY.

Kaufman L, Rousseeuw P (1990) Finding groups in data: an introduction for cluster analysis. Wiley, New York, NY.

Kawai M, Ohsawa H, Mori U, Dunbar RIM (1983) Social organization of gelada baboons: social units and definitions. Primates 24:13–24.

Kershenbaum A (2014) Entropy rate as a measure of animal vocal complexity. Bioacoustics 23:195–208.

Kershenbaum A, Blumstein DT, Roch MA, Akçay Ç, Backus G, Bee MA, Bohn K, Cao Y, Carter G (2016) Acoustic sequences in non-human animals: a tutorial review and prospectus. Biol Rev 91:13–52.

Kershenbaum A, Bowles AE, Freeberg TM, Jin DZ, Lameira AR, Bohn K (2014) Animal vocal sequences: not the Markov chains we thought they were. Proc R Soc B 281:20141370.

Koda H (2004) Flexibility and context-sensitivity during the vocal exchange of coo calls in wild Japanese macaques (*Macaca fuscata yakui*). *Behaviour* 141:1279–1296.

Koda H, Lemasson A, Oyakawa C, Rizaldi, Pamungkas J, Masataka N (2013) Possible role of mother-daughter vocal interactions on the development of species specific song in gibbons. Plos One 8:e71432.

Koda H, Oyakawa C, Kato A, Masataka N (2007) Experimental evidence to the volitional control of vocal production in an immature gibbon. Behaviour 144:681–692.

Krams I, Krama T, Freeberg TM, Kullberg C, Lucas JR (2012) Linking social complexity and vocal complexity: a parid perspective. Philos Trans R Soc B 367:1879–1891.

Krebs JR, Davies NB, Parr J (1993) An introduction to behavioural ecology, 3rd ed. Blackwell, Oxford.

Krebs JR, Dawkins R (1984) Animal signals: mind-reading and manipulation. In: JT Krebs, NB Davies (eds), Behavioural ecology: an evolutionary approach, 2nd ed. Blackwell, Oxford, pp 380–402.

Kroodsma DE (1977) Correlates of song organization among north American wrens. Am Nat 111:995–1008.

Kumar R, Sinha A, Radhakrishna S (2013) Comparative demography of two commensal macaques in India: implications for population status and conservation. Folia Primatol 84:384–393.

Ladyman J, Lambert J, Wiesner K (2013) What is a complex system? Eur J Phil Sci 3: 33–67.

Laland K (2017) Darwin's unfinished symphony: how culture made the human mind. Princeton University Press, Princeton, NJ.

Lamarck JB (1809) Philosophie zoologique. Dentu, Paris.

Lameira AR (2017) Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. Neurosci Biobehav Rev 83:429–439.

Lameira AR, Hardus ME, Kowalsky B, de Vries H (2013*)* Orangutan (*Pongo* spp.) whistling and implications for the emergence of an open-ended call repertoire: a replication and extension. J Acoust Soc Am 134:1–11.

Lameira AR, Hardus ME, Mielke A, Wich SA, Shumaker RW (2016) Vocal fold control beyond the species-specific repertoire in an orang-utan. Sci Rep 6:30315.

Landeau L, Terborgh J (1986) Oddity and the "confusion effect" in predation. Anim Behav 34:1372–1380.

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18.

Lehmann J, Dunbar RIM (2009) Network cohesion, group size and neocortex size in female-bonded old world primates. Proc R Soc B 276:4417–4422.

Leighton GM (2017) Cooperative breeding influences the number and type of vocalizations in avian lineages. Proc R Soc B 284:20171508.

Lemasson A, Blois-Heulin C, Jubin R, Hausberger M (2006) Female social relationships in a captive group of Campbell's monkeys (*Cercopithecus campbelli campbelli*). Am J Primatol 68:1161–1170.

Lemasson A, Guilloux M, Rizaldi, Barbu S, Lacroix A, Koda H (2013a) Age- and sex-dependent contact call usage in Japanese macaques. Primates 54:283–291.

Lemasson A, Hausberger M (2004) Patterns of vocal sharing and social dynamics in a captive group of Campbell's monkeys. J Comp Psychol 118:347–359.

Lemasson A, Hausberger M (2011) Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). Acoust Soc Am 129:3341–3352.

Lemasson A, Jubin R, Masataka N, Arlet M (2016) Copying hierarchical leaders' voices? Acoustic plasticity in female Japanese macaques. Sci Rep 6:21289.

Lemasson A, Ouattara K, Bouchet H, Zuberbühler K (2010) Speed of call delivery is related to context and caller identity in Campbell's monkey males. Naturwissenschaften 97:1023–1027.

Lemasson A, Ouattara K, Petit EJ, Zuberbühler K (2011) Social learning of vocal structure in a nonhuman primate? BMC Evol Biol 11:362.

Lemasson A, Ouattara K, Zuberbühler K (2013b) Exploring the gaps between primate calls and human language. In: R Botha, M Everaert (eds), The evolutionary emergence of language, evidence and inference. Oxford University Press, Oxford, pp 181–203.

Lemasson A, Remeuf K, Rossard A, Zimmermann E (2012) Cross-taxa similarities in affect-induced changes of vocal behavior and voice in arboreal monkeys. Plos One 7:7–12.

Lenth R, Singmann H, Love J (2018) Eemmeans: estimated marginal means, aka least-squares means. https://cran.r-project.org/web/packages/emmeans/index.html

Levréro F, Carrete-Vega G, Herbert A, Lawabi I, Courtiol A, Willaume E, Kappeler PM, Charpentier MJE (2015) Social shaping of voices does not impair phenotype matching of kinship in mandrills. Nat Commun 6:7609.

Levréro F, Touitou S, Frédet J, Nairaud B, Guéry JP, Lemasson A (2019) Social bonding drives vocal exchanges in bonobos. Sci Rep 9:711.

Lewis SA (1985) The vocal repertoire of the Ccelebes black ape (*Macaca nigra*). University of Georgia, Athens, GA.

Liebal K, Waller BM, Burrows AM, Slocombe KE (2012) Primate communication: a multimodal approach. Cambridge University Press, Cambridge.

Lieberman PH, Klatt DH, Wilson WH (1969) Vocal tract limitations on the vowel repertoires of rhesus monkey and other nonhuman primates. Science 164:1185–1187.

Limoges C (1994) Milne-Edwards, Darwin, Durkheim and the division of labour: a case study in reciprocal conceptual exchanges between the social and the natural sciences. In: IB Cohen (ed.), The natural sciences and the social sciences: some critical and historical perspectives. Kluwer Academic, Dordrecht, pp 317–343.

Lindburg DG (1971) The rhesus monkey in North India: an ecological and behavioural study. In: LA Rosenblum (ed), Primate behavior: developments in field and laboratory research, Vol 2. Academic Press, New York, NY, pp 1–106.

Lucas JR, Gentry KE, Sieving KE, Freeberg TM (2018) Communication as a fundamental part of machiavellian intelligence. J Comp Psychol 132:442–454.

Macedonia JM, Evans CS (1993) Essay on contemporary issues in ethology: variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93:177–197.

Maciej P, Ndao I, Hammerschmidt K, Fischer J (2013) Vocal communication in a complex multi-level society: constrained acoustic structure and flexible call usage in Guinea baboons. Front Zool 10:58.

MacLean EL, Merritt DJ, Brannon EM (2008) Social complexity predicts transitive reasoning in prosimian primates. Anim Behav 76:479–486.

Maeda T, Masataka N (1987) Locale-specific vocal behaviour of the tamarin (*Saguinus I. labiatus*). Ethology 75:25–30.

Manser MB, Jansen DAWAM, Graw B, Hollén LI, Bousquet CAH, Furrer, RD, le Roux A (2014) Vocal complexity in meerkats and other mongoose species. Adv Study Behav 46:281–310.

Manson JH (2010) Mate choice. In: C Campbell, A Fuentes, S MacKinnon, R Stumpf (eds), Primates in perspective. Oxford University Press, Oxford, pp 476–488.

Marler P (1955) Characteristics of some animal calls. Nature 176:6–8.

Marler P (1967) Animal communication signals. Science 157:769–774.

Marler P, Evans CS, Hauser MD (1992) Animal signals: motivational, referential, or both. In: H Papousek, U Jürgens, M Papousek (eds), Nonverbal vocal communication: comparative and developmental approaches. Cambridge University Press, Cambridge, pp 66–86.

Marler P, Slabbekoorn H (2004) Nature's music: the science of birdsong. Elsevier Academic Press, San Diego, CA.

Marler P, Tamura M (1964) Culturally transmitted patterns of vocal behavior in sparrows. Science 146:1483–1486.

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization - I. Temperate habitats. Behav Ecol Sociobiol 2:271–290.

Martin Mäaechler M, Rousseeuw P, Struyf A, Hubert M (2018) Cluster: cluster analysis basics and extensions. R package Version 2.0.1., https://svn.r-project.org/R-packages/trunk/cluster

Masataka N, Thierry B (1993) Vocal communication of Tonkean macaques in confined environments. Primates 34:169–180.

Mates EA, Tarter RR, Ha JC, AB Clark AB , KJ McGowan KJ (2015) Acoustic profiling in a complexly social species, the American crow: caws encode information on caller sex, identity and behavioural context. Bioacoustics 24:63–80.

Matsumura S (1999) The evolution of "egalitarian" and "despotic" social systems among macaques. Primates 40:23–31.

May-Collado LJ, Agnarsson I, Wartzok D (2007) Phylogenetic review of tonal sound production in whales in relation to sociality. BMC Evol Biol 7:136.

Maynard Smith J, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolper, L (1985) Developmental constraints and evolution. Q Rev Biol 60:265–287.

Maynard Smith J, Szathmáry E (1995) The major transitions in evolution. Oxford University Press, Oxford.

McComb K, Semple S (2005) Coevolution of vocal communication and sociality in primates. Biol Lett 1:381–385.

McDaniel RRJ, Driebe DJ, eds (2005) Uncertainty and surprise in complex systems: questions on working with the unexpected. Springer, Berlin.

McLennan DA, Brooks DR (2002) Complex histories of speciation and dispersal in communities: a re-analysis of some Australian bird data using BPA. J Biogeogr 29:1055–1066.

McNicholas PD (2016) Model-based clustering. J Classif 33:331–373.

McShea DW (1991) Complexity and evolution: what everybody knows. Biol Philos 6:303–324.

McShea DW (1996) Metazoan complexity and evolution: is there a trend? Evolution 50: 477–492.

McShea DW (2001) The hierarchical structure of organisms: a scale and documentation of a trend in the maximum. Paleobiology 27: 405–423.

Ménard N (2004) Do ecological factors explain variation in social organization ? In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 237–266.

Micheletta J (2012) Social communication in crested macaques (*Macaca nigra*). PhD thesis, University of Portsmouth, Portsmouth.

Micheletta J, Engelhardt A, Matthews L, Agil M, Waller BM (2013) Multicomponent and multimodal lipsmacking in crested macaques (*Macaca nigra*). Am J Primatol 75:763–773.

Micheletta J, Waller BM, Panggur MR, Neumann C, Duboscq J, Agil M, Engelhardt A (2012) Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. Proc R Soc B 279:4042–4050.

Micheletta J, Whitehouse J, Parr LA, Waller BM (2015) Facial expression recognition in crested macaques (*Macaca nigra*). Anim Cogn 18:985–990.

Miller CT, Flusberg S, Hauser MD (2003) Interruptibility of long call production in tamarins: implications for vocal control. J Exp Biol 206:2629–2639.

Mitani JC (1988) Male gibbon (*Hylobates agilis*) singing behavior: natural history, song variations and function. Ethology 79:177–194.

Mitani JC, Gros-Louis J (1998) Chorusing and call convergence in chimpanzees: tests of three hypotheses. Behaviour 135:1041–1064.

Mitani JC, Hasegawa T, Gros-Louis J, Marler P, Byrne RW (1992) Dialects in wild chimpanzees? Am. J. Primatol 27:233–243.

Mohamad I BinB, Usman D (2013) Standardization and its effects on K-means clustering algorithm. Res J Appl Sci Eng Technol 6:3299–3303.

Morales JC, Melnick DJ (1998) Phylogenetic relationships of the macaques (*Cercopithecidae*: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. J Hum Evol 34:1–23.

Morton ES (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am Nat 111:855–869.

Muroyama Y, Thierry B (1998) Species differences of male loud calls and their perception in Sulawesi macaques. Primates 39:115–126.

Muthukrishna M, Shulman BW, Vasilescu V, Henrich J (2014) Sociality influences cultural complexity. Proc R Soc B 281: 20132511

Naik GR (2017) Advances in principal component analysis. Springer, Singapore.

Nakagawa N, Matsubara M, Shimooka Y, Nishikawa M (2015) Embracing in a wild group of Yakushima macaques (*Macaca fuscata yakui*) as an example of social customs. Curr Anthropol 56: 104–120.

Neefe JR, Ellis EB, Rogentine GN (1975) Rhesus lymphocyte alloantigens. III. Identification of new antigen. Tiss Antig 6:195–204

Nettle D (2012) Social scale and structural complexity in human languages. Phil Trans R Soc B 367:1829–1836.

Newman JD, Symmes D (1982) Inheritance and experience in the acquisition of primate acoustic behavior. In: CT Snowdon, CH Brown, MR Peterson (eds), Primate communication. Cambridge University Press, Cambridge, pp 259–278.

Nishimura T, Oishi T, Suzuki J, Matsuda K, Takahashi T (2008) Development of the supralaryngeal vocal tract in Japanese macaques: implications for the evolution of the descent of the larynx. Am J Phys Anthropol 135:182–194.

Norconk MA (2007) Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed predators. In: CJ Campbell, A Fuentes, K MacKinnon, M Panger, SK Bearder (eds), Primates in perspective. Oxford University Press, Oxford, pp 123–138.

O'Brien TG, Kinnaird MF (1997) Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). Int J Primatol 18:321–351.

Ord TJ, Garcia-Porta J (2012) Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups. Phil Trans R Soc B 367:1811–1828.

Ordóñez-Gómez JD, Santillán-Doherty AM, Fischer J, Hammerschmidt K (2018) Acoustic variation of spider monkeys' contact calls (whinnies) is related to distance between vocalizing individuals and immediate caller behavior. Am J Primatol 80:1–11.

Ossi K, Kamilar JM (2006) Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: *Lemuridae*). Behav Ecol Sociobiol 61:53–64.

Ouattara K, Lemasson A, Zuberbühler K (2009) Campbell's monkeys concatenate vocalizations into context-specific call sequences. Proc Natl Acad Sci USA 106:22026–22031.

Owren MJ, Dieter JA, Seyfarth RM, Cheney DL (1992) "Food" calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross-fostered between species. Behaviour 120:218–231.

Owren MJ, Dieter JA, Seyfarth RM, Cheney DL (1993) Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. Dev Psychobiol 26:389–406.

Owren MJ, Rendall D (1997) An affect-conditioning model of nonhuman primate vocal signaling. In: DH Owings DH, MD Beecher MD, NS Thompson NS (eds), Communication. Springer, Berlin, pp 299–346.

Owren MJ, Rendall D (2001) Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. Evol Anthropol 10:58–71.

Page SE (2011) Complexity and diversity, Vol 2. Princeton University Press, Princeton, NJ.

Page SE (2011) Diversity and complexity, (Vol. 2). Princeton University Press, Princeton, NJ.

Palagi E, Dall'Olio S, Demuru E, Stanyon R (2014) Exploring the evolutionary foundations of empathy: consolation in monkeys. Evol Hum Behav 35:341–349.

Palombit RA (1992) A preliminary study of vocal communication in wild long-tailed macaques (*Macaca fascicularis*). II. Potential of calls to regulate intragroup spacing. Int J Primatol 13:183–207.

Palombit RA (1996) Pair bonds in monogamous apes: a comparison of the siamang *Hylobates syndactylus* and the white-handed gibbon *Hylobates lar.* Behaviour 133:321–356.

Panggur MR (2014) Vocal communication of wild crested macaque (*Macaca nigra*). MS thesis, Bogor Agricultural University, Bogor.

Pardo JS, Gibbons R, Suppes A, Krauss RM (2012) Phonetic convergence in college roommates. J. Phon 40:190–197.

Parrish J, Viscido S, Grünbaum D (2002) Self-organized fish schools: an examination of emergent properties. Biol Bull 202:296–305.

Patzelt A, Kopp GH, Ndao I, Kalbitzer U, Zinner D, Fischer J (2014) Male tolerance and male–male bonds in a multilevel primate society. Proc Natl Acad Sci USA 11114740–14745.

Paul A (2004) Dominance and paternity. In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 131–134.

Peckre L, Kappeler PM, Fichtel C (2019) Clarifying and expanding the social complexity hypothesis for communicative complexity. Behav Ecol Sociobiol 73:11.

Peckre LR, Kappeler PM, Fichtel C (2019) Clarifying and expanding the social complexity hypothesis for communicative complexity. Behav Ecol Sociobiol 73:5.

Peet RK (1974) The measurement of species diversity. Ann Rev Ecol Syst 5: 285–307.

Peters EH (1983) Vocal communication in an introduced colony of feral rhesus monkeys (*Macaca mulatta*). PhD, University of Florida, FL.

Petit O, Bertrand F, Thierry B (2008) Social play in crested and Japanese macaques: testing the covariation hypothesis. Dev Psychobiol 50:399–407.

Petit O, Desportes C, Thierry B (1992) Differential probability of 'coproduction' in two species of macaque (*Macaca tonkeana*, *M. mulatta*). Ethology 90:107–120.

Petit O, Thierry B (1994) Aggressive and peaceful interventions in conflicts in Tonkean macaques. Anim Behav 48:1427–1436.

Petit O, Thierry B (2000) Do impartial interventions occur in monkeys and apes? In: F Aureli, FBM de Waal (eds), Natural conflict resolution. University of California Press, Berkeley, CA, pp 267–269.

Pfefferle D, Hammerschmidt K, Mundry R, Ruiz-Lambides AV, Fischer J, Widdig A (2016) Does the structure of female rhesus macaque coo calls reflect relatedness and/or familiarity? Plos One 11:e0161133.

Pfefferle D, Heistermann M, Hodges JK, Fischer J (2008) Male Barbary macaques eavesdrop on mating outcome: a playback study. Anim Behav 75:1885–1891.

Pielou EC (1969) An introduction to mathematical ecology. John Wiley, Hoboken, NJ.

Pika S (2017) Unpeeling the layers of communicative complexity. Anim Behav 134:223–227.

Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. Am J Primatol 60:95–111.

Pollard KA, Blumstein DT (2012) Evolving communicative complexity: insights from rodents and beyond. Phil Trans R Soc B 367:1869–1878.

Pombo AR, Waltert M, Mansjoer SS, Mardiastuti A, Mühlenberg M (2004) Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: G Gerold, M Fremerey, E Guhardja (eds), Land use, nature conservation, and the stability of rainforest margins in southeast Asia. Springer, Berlin, pp 313–325.

Powell LE, Isler K, Barton RA (2017) Re-evaluating the link between brain size and behavioural ecology in primates. Proc R Soc B 284:1–8.

Pozzi L, Gamba M, Giacoma C (2010) The use of artificial neural networks to classify primate vocalizations: a pilot study on black lemurs. Am J Primatol 72:337–348.

Preuschoft S (2004) Power and communication. In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 58–60.

Preuschoft S, van Schaik CP (2000) Dominance and communication. In: F Aureli, FBM de Waal (eds), Natural conflict resolution. University of California Press, California, CA, pp 77–105.

Price T, Fischer J (2014) Meaning attribution in the West African green monkey: influence of call type and context. Anim Cogn 17:277–286.

Price T, Wadewitz P, Cheney D, Seyfarth R, Hammerschmidt K, Fischer J (2015) Vervets revisited: a quantitative analysis of alarm call structure and context specificity. Sci Rep 5:1–11.

Puga-Gonzalez I, Butovskaya M, Thierry B, Hemelrijk CK (2014) Empathy versus parsimony in understanding post-conflict affiliation in monkeys: model and empirical data. Plos One 9:1–7.

Purvis A (1995) A composite estimate of primate phylogeny. Phil Trans R Soc B 348:405–421.

R Core Team (20187). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Radespiel U (2000) Sociality in the gray mouse lemur (*Microcebus murinus*) in northwestern Madagascar. Am J Primatol 51:21–40.

Ramos-Fernandez G, King AJ, Beehner JC, Bergman TJ, Crofoot MC, Di Fiore A, Lehmann J, Schaffner CM, Snyder-Mackler N, Zuberbühler K, Aureli F, Boyer D (2018) Quantifying uncertainty due to fission–fusion dynamics as a component of social complexity. Proc R Soc B 285:20180532.

Range F, Fisher J (2004) Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. Ethology 110:301–321.

Rebout N, Desportes C, Thierry B (2017) Resource partitioning in tolerant and intolerant macaques. Aggress Behav 43:513–520.

Redondo T, De Reyna LA (1988) Locatability of begging calls in nestling altricial birds. Anim Behav 36:653–661.

Rendall D (2003) Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. J Acoust Soc Am 113:3390–3402.

Rendall D, Owren MJ, Weerts E, Hienz RD (2004) Sex differences in the acoustic structure of vowel-like grunt vocalizations in baboons and their perceptual discrimination by baboon listeners. J Acoust Soc Am 115:411–421.

Rendall D, Seyfarth RM, Cheney DL, Owren MJ (1999) The meaning and function of grunt variants in baboons. Anim Behav 57:583–592.

Rice AN, Land BR, Bass AH (2011) Nonlinear acoustic complexity in a fish "two-voice" system. Proc R Soc B 278:3762–3768.

Richard JP (1991) Sound analysis and synthesis using an Amiga micro-computer. Bioacoustics 3:45–60.

Riede T, Owren MJ, Arcadi AC (2004) Nonlinear acoustics in pant hoots of common chimpanzees (*Pan troglodytes*): frequency jumps, subharmonics, biphonation, and deterministic chaos. Am J Primatol 64:277–291.

Riley EP (2005) The loud call of the Sulawesi Tonkean macaque, *Macaca tonkeana*. Trop Biodiv 8:199–209.

Riley EP (2007) Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. Int J Primatol 28:107–133.

Robbins MM (2007) Gorillas: diversity in ecology and behavior. In: CJ Campbell, A Fuentes, K MacKinnon, M Panger, SK Bearder (eds), Primates in perspective. Oxford University Press, Oxford. pp 305–321.

Romano V, Duboscq J, Sarabian C, Thomas E, Sueur C, MacIntosh AJ (2016) Modeling infection transmission in primate networks to predict centrality-based risk. Am J Primatol 78:767–779.

Rosenbaum B, O'Brien TG, Kinnaird MF, Supriatna J (1998) Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: effects of habitat disturbance and hunting. Am J Primatol 44:89–106.

Roskaft E, Espmark Y (1982) Vocal communication by the rook *Corvus frugilegus* during the breeding season. Ornis Scand 13:38–46.

Roush RS, Snowdon CT (2000) Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. Ethology 106:673–690.

Rowell TE, Hinde RA (1962) Vocal communication by rhesus monkey (*Macaca mulatta*). Proc Zool Soc London 138:279–294.

Roy S, Miller CT, Gottsch D, Wang X (2011) Vocal control by the common marmoset in the presence of interfering noise. J Exp Biol 214:3619–3629.

Ruxton GD (2009) Non-visual crypsis: a review of the empirical evidence for camouflage to senses other than vision. Phil Trans R Soc B 364:549–557.

Sampson G, Gil D, Trudgill P (2009) Language complexity as an evolving variable. Oxford University Press, Oxford.

Samuel V. Scarpino, Gillette R, Crews D (2013) MmultiDimBio: an R package for the design, analysis, and visualization of systems biology experiments.

http://cran.r-project.org/web/packages/multiDimBio/index.html

Scarantino A, Clay Z (2015) Contextually variable signals can be functionally referential. Anim Behav 100:1–8.

Schaum N, Karkanias J, Neff NF, May AP, Quake SR, Wyss-Coray T, et al (2018) Single-cell transcriptomics of 20 mouse organs creates a *Tabula Muris*. Nature 562:367–372.

Schlenker P, Chemla E, Arnold K, Lemasson, A, Ouattara K, Keenan S, Stephan C, Ryder R, Zuberbühler K (2014) Monkey semantics: two "dialects" of Campbell's monkey alarm calls. Ling Phil 37:439–501.

Schlichting CD, Pigliucci M (1998) Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, MA.

Schradin C, Hayes ND, Pillay N, Bertelsmeier C (2018) The evolution of intraspecific variation in social organization. Ethology 124: 527–536

Schradin C, Schmohl G, Rödel HG, ScChoepf I, Treffler SM, Brenner J, Bleeker M, Schubert M, König B, Pillay N (2010) Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. Anim Behav 79:195–203.

Schuster P (2016) How complexity originate. Examples from history reveal additional roots to complexity. Complexity 21:7–12.

Scopa C, Palagi E (2016) Mimic me while playing! Social tolerance and rapid facial mimicry in macaques. J Comp Psychol 130:153–161.

Scrucca L, Fop M, Murphy TB, Raftery AE (2016) Mmclust 5: clustering, classification and density estimation using Gaussian finite mixture models. R J 8:289–317.

Seyfarth RM, Cheney DL (2003) Meaning and emotion in animal vocalizations. Ann N Y Acad Sci 1000:32–55.

Seyfarth RM, Cheney DL (2017) The origin of meaning in animal signals. Anim Behav 124:339–346.

Seyfarth RM, Cheney DL, Bergman TJ, Fischer J (2010) The central importance of information in studies of animal communication. Anim Behav 80:3–8.

Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: eEvidence of predator classification and semantic communication. Science 210:801–803.

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423.

Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana, IL.

Sheets E, Craighead WE (2007) Toward an empirically based classification of personality pathology. Clin Psychol Sci Pract 14:77–93.

Shultz S, Dunbar RIM (2006) Chimpanzee and felid diet composition is influenced by prey brain size. Biol Lett 2:505–508.

Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. Nature 479:219–222.

Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro S (2013) Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. Anim. Behav 85: 941–947.

Silk JB, Kaldor E, Boyd R (2000) Cheap talk when interests conflict. Anim Behav 59:423–432.

Silk JB, Seyfarth RM, Cheney DL (2016) Strategic use of affiliative vocalizations by wild female baboons. Plos One 11:1–10.

Skyrms B (2010) Signals: evolution, learning, and information. Oxford University Press, Oxford.

Slocombe KE, Zuberbühler K (2006) Food-associated calls in chimpanzees: responses to food types or food preferences? Anim Behav 72:989–999.

Slocombe KE, Zuberbühler K (2007) Chimpanzees modify recruitment screams as a function of audience composition. Proc Natl Acad Sci USA 104:17228–17233.

Smith RJF (1977) Chemical communication as adaptation: alarm substance of fish. In: D Müller-Schwarze (ed), Chemical signals in vertebrates. Plenum Press, New York, NY, pp 303–320

Smith WJ (1965) Message, meaning, and context in ethology. Am Nat 99:405–409.

Snowdon CT (2017) Learning from monkey "talk". Science 335:1120–1122.

Snowdon CT, Elowson AM (1999) Pygmy marmosets modify call structure when paired. Ethology 105:893–908.

Snowdon CT, Hausberger M, eds (1997) Social influences of vocal development. Cambridge University Press, Cambridge.

Soltis J (2004) Mating systems. In: B Thierry, M Singh, W Kaumanns (eds), Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 135–151

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309.

Struhsaker TT (1967) Auditory communication among vervet monkeys (*Cercopithecus aetthiops*). In: SA Altmann (ed), Social communication among primates. University of Chicago Press, Chicago, IL, pp 281–324.

Stumpf R (2007) Chimpanzees and bonobos: diversity within and between species. In: CJ Campbell, A Fuentes, K MacKinnon, M Panger, SK Bearder (eds), Primates in perspective. Oxford University Press, Oxford, pp 321–344.

Sugiura H (1998) Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. Anim Behav 55:673–687.

Sugiura H (2007) Adjustment of temporal call usage during vocal exchange coo calls in Japanese macaques. Ethology 113:528–533.

Sutton D, Larson C, Taylor EM, Lindeman RC (1973) Vocalization in rhesus monkeys: conditionability. Brain Res 52:225–231.

Taborsky B, Oliveira RF (2012) Social competence: an evolutionary approach. Trends Ecol Evol 27:679–688.

Taglialatela JP, Russell JL, Schaeffer JA, Hopkins WD (2008) Communicative signaling activates Broca' s' homolog in chimpanzees. Curr Biol 18: 343–348.

Takahashi T, Higashino A, Takagi K, Kamanaka Y, Abe M, Morimoto M, Kang KH, Goto S, Suzuki J, Hamada Y, Kageyama T (2006) Characterization of obesity in Japanese monkeys (*Macaca fuscata*) in a pedigreed colony. J Med Primatol 35:30–37.

Tanaka T, Sugiura H, Masataka N (2006) Cross-sectional and longitudinal studies of the development of group differences in acoustic features of coo calls in two groups of Japanese macaques. Ethology 112:7–21.

Thierry B (1985) Patterns of agonistic interactions in three species of macaque (*Macaca mulatta, M fascicularis, M tonkeana*). Aggress Behav 11:223–233.

Thierry B (1990) Feedback loop between kinship and dominance: the macaque model. J Theor Biol 145:511–522.

Thierry B (1994) Social transmission, tradition and culture in primates: from the epiphenomenon to the phenomenon. Techn Cult 23/24: 91–119.

Thierry B (2000) Covariation of conflict management patterns across macaque species. In: F Aureli, FBM de Waal (eds), Natural conflict resolution. University of California Press, California, CA, pp 106–128.

Thierry B (2007) Unity in diversity: lessons from macaque societies. Evol Anthropol 16:224–238.

Thierry B (2008) Primate socioecology, the lost dream of ecological determinism. Evol Anthropol 17:93–96.

Thierry B (20112010) The macaques: a double-layered social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds), Primates in perspective. Oxford University Press, Oxford, pp 229–241.

Thierry B (2013) Identifying constraints in the evolution of primate societies. Phil Trans R Soc B 368:20120342.

Thierry B, Anderson JR, Demaria C, Desportes C, Petit O (1994) Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: JJ Roeder, B Thierry, JR Anderson, N Herrenschmidt (eds), Current primatology, Vol 2: Social development, learning and behaviour. Université Louis Pasteur, Strasbourg, pp 103–117.

Thierry B, Aureli F, Nunn CL, Petit O, Abegg C, de Waal FBM (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. Anim Behav 75:847–860.

Thierry B, Bynum EL, Baker S, Kinnaird MF, Matsumura S, Muroyama Y, O'Brien TG, Petit O, Watanabe K (2000) The social repertoire of Sulawesi macaques. Primate Res 16:203–226.

Thierry B, Demaria C, Preuschoft S, Desportes C (1989) Structural convergence between silent bared teeth display and relaxed open mouth display in Tonkean mMacaque (*Macaca tonkeana*). Folia Primatol 52:178–184.

Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behaviour of macaques (Primates: *Cercopithecidae*, genus *Macaca*). Ethology 106:713–728.

Tokuda I, Riede T, Neubauer J, Owren MJ, Herzel H (2002) Nonlinear analysis of irregular animal vocalizations. J Acoust Soc Am 111:2908–2919.

Tomasello M (2008) Origins of human communication. MIT Press/Bradford Books, Cambridge, MA.

Tosi AJ, Morales JC, Melnick DJ (2003) Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. Evolution 57:1419–1435.

Tseng W-S (2001) Handbook of cultural psychiatry. Academic Press, San Diego, CA.

Turchin P, Currie TE, Whitehouse H, François P, Feeney K, et al (2017) Quantitative historical analysis uncovers a single dimension of complexity that structures global variation in human social organization. Proc Natl Acad Sci USA 115:E144–E151.

Tyack PL (2008) Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. J Comp Psychol 122:319–340.

Valentine JW, Collins AG, Meyer CP (1994) Morphological complexity increase in metazoans. Paleobiology 20:131–142.

van Noordwijk M, van Schaik CP (2004) Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: PM Kappeler, CP van Schaik (eds), Sexual selection in primates: new and comparative perspectives. Cambridge University Press, Cambridge, pp 208–229.

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: V Standen, RA Foley (eds), Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell, Cambridge, pp 195–218.

van Schaik CP, van Hooff J (1983) On the ultimate causes of primate social systems. Behaviour 85:91–117.

Vanden Hole C, Van Daele PAAG, Desmet N, Devos P, Adriaens D (2013) Does sociality imply a complex vocal communication system? A case study for *Fukomys micklemi* (*Bathyergidae*, *Rodentia*). Bioacoustics 23:143–160.

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th ed. Springer, New York, NY.

Volodin IA, Volodina EV, Lapshina EN, Efremova KO, Soldatova NV (2014) Vocal group signatures in the goitred gazelle *Gazella subgutturosa*. Anim. Cogn 17:349–357.

von Bertalanffy L (1968) General system theory. George Braziller, New York, NY.

Wadewitz P, Hammerschmidt K, Battaglia D, Witt A, Wolf F, Fischer J 2015) Characterizing vocal repertoires - – Hard vs. soft classification approaches. Plos One 10:e0125785.

Waser PM, Brown CH (1986) Habitat acoustics and primate communication. Am J Primatol 10:135–154.

Watson SK, Townsend SW, Schel AM, Wilke C, Wallace EK, Cheng L, West V, Slocombe KE (2015) Vocal learning in the functionally referential food grunts of chimpanzees. Curr Biol 25:495–499.

Weiss MN, Franks DW, Croft DP, Whitehead H (2019) Measuring the complexity of social associations using mixture models. Behav Ecol Sociobiol 73:8.

Wen X, Fuhrman S, Michaels GS, Carr DB, Smith S, Barker JL, Somogyi R (1998) Large-scale temporal gene expression mapping of central nervous system development. Proc Natl Acad Sci USA 95:334–339.

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, Oxford.

Wheeler BC, Fischer J (2012) Functionally referential signals: a promising paradigm whose time has passed. Evol Anthropol 21:195–205.

Wheeler BC, Hammerschmidt K (2013) Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? Am J Primatol 75:715–725.

Whitehead H (2009) SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol 63: 765–778.

Whitehouse H, François P, Savage PE, Currie TE, Feeney KC, Cioni E, Purcell R, Ross RM, Larson J, Baines J, ter Haar B, Covey A, Turchin P (2019) Complex societies precede moralizing gods throughout world history. Nature 568: 226–229.

Whiten A, Byrne RW (1997) Machiavellian intelligence II : extensions and evaluations. Cambridge University Press, Cambridge.

Wilbrecht L, Nottebohm F (2003) Vocal learning in birds and humans. Ment Retar Dev Dis Res Rev 9: 135–148.

Wiley RH (2012) Communication as a transfer of information: measurement, mechanism and meaning. In: UE Stegmann (ed), Animal communication theory: information and influence. Cambridge University Press, Cambridge, pp 113–129.

Wilkinson GS (2003) Social and vocal complexity in bats. In: FBM de Waal, PL Tyack (eds), Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA, pp 322–341.

Wilkinson GS, Boughman JW (1998) Social calls coordinate foraging in greater spear-nosed bats. Anim. Behav 55:337–350.

Wilkinson GS, Carter GG, Bohn KM (2019) Kinship, association and social complexity in bats. Behav Ecol Sociobiol 73:1–15.

Wilson DR, Hare JF (2004) Ground squirrel uses ultrasonic alarms. Nature 430:523.

Wilson E (1975) Sociobiology: the new synthesis. Belknap Press of Harvard University Press, Cambridge, MA.

Wimsatt WC, Schank JC (2004) Generative entrenchement, modularity and evolvability: when genic selection meets the whole organism. In: G Schlosser, G Wagner (eds), Modularity in development and evolution. University of Chicago Press, Chicago, IL, pp 359–394.

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300.

Yoshida S, Okanoya K (2005) Evolution of turn-taking: a bio-cognitive perspective. Cogn Stud 12:153–165.

Zannella A, Stanyon R, Palagi E (2017) Yawning and social styles: different functions in tolerant and despotic macaques (*Macaca tonkeana* and *Macaca fuscata*). J Comp Psychol 131:179–188.

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10.

Ziegler T, Abegg C, Meijaard E, Perwitasari-Farajallah D, Walter L, Hodges JK, Roos C (2007) Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. Mol Phylogen Evol 42:807–816.

Zuberbühler K (2000) Interspecies semantic communication in two forest primates. Proc R Soc B 267:713–718.

Zuberbühler K (2008) Quick guides audience effects. Curr Biol 18:189–190.

Zuberbühler K, Noë R, Seyfarth RM (1997) Diana monkey long-distance calls: messages for conspecifics and predators. Anim Behav 53:589–604.

APPENDIX publications outside the scope of the thesis

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RESEARCH ARTICLE

WILEY AGGRESSIVE BEHAVIOR

Resource partitioning in tolerant and intolerant macaques

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The clumped distribution of food resources promotes food defensibility and can lead to the monopolizing of resources by high-ranking individuals. However, the balance of power is set at different levels according to societies, meaning that resource partitioning should vary between them. This study investigates whether dominance asymmetry and resource partitioning are related in non-human primates by comparing two species with contrasting social styles, namely rhesus macaques (*Macaca mulatta*) which display strong social intolerance and a steep gradient of dominance, and Tonkean macaques (*Macaca tonkeana*), which exhibit higher levels of tolerance and more balanced dominance relationships. Study groups were kept in semi-free ranging conditions. Animals were provided with fruit in three different clumped conditions during 30-min trials. We found that higher-ranking rhesus macaques had priority for the access to fruit: these individuals spent longer in the feeding area in the first 10-min period of trials, while lower-ranking individuals had diminished access to fruit under the most clumped condition; this was associated with sustained agonistic interactions. Dominance effects were weaker in Tonkean macaques. They exhibited co-feeding between high- and low-ranking individuals in the first period; there was no significant effect of dominance even in the most clumped condition; and frequencies of agonistic interactions remained moderate relative to the number of individuals present in the feeding area. These results show that food resources were more equitably distributed among group members in tolerant macaques than in their intolerant counterparts. Dominance gradient and social tolerance may be considered as two aspects of the same phenomenon.

KEYWORDS
competition, dominance, primates, social style, tolerance

1 | INTRODUCTION

Power inequality is a major feature of social life in humans and other primates (Chapais, 1991; Kurtz, 2001; Mattison, Smith, Shenk, & Cochrane, 2016; Watts, 2010). By living together, individuals are safer from predators and cooperate to find and defend resources. However, group living increases local population density, enhancing the intensity of intraspecific competition and accentuating inequalities among individuals (Alexander, 1974; Janson & van Schaik, 1988). For instance, increased group size in non-human primates results in longer foraging activities and shorter feeding bouts due to heightened food competition (Majolo, de Bortoli Vizioli, & Schino, 2008; Nakagawa, 1990). According to socio-ecological theory, patterns of competition are shaped by the availability, distribution, and quality of food: when food resources are of low nutritional value or dispersed, intragroup competition is expected to be limited, whereas the concentration of resources such as fruit trees in discrete, high-quality patches promotes food defensibility, meaning that higher-ranking individuals can monopolize access to resources at the expense of others (Clutton-Brock & Janson, 2012; Isbell, 1991; Sterck, Watts, & van Schaik, 1997).

In experimental conditions, the distribution of food in a limited area increases social tension and levels of agonistic behaviors (Belzung & Anderson, 1986; Boccia, Laudenslager, & Reite, 1988; Chancellor & Isbell, 2008; de Waal, 1984; Southwick, 1967): like in natural conditions, the dominant individuals obtain a larger share of resources by controlling access to the feeding site through aggression and/or staying close to the food, and group members enter the feeding site in order of their dominance status (Belzung & Anderson, 1986; Boccia et al., 1988; Brennan & Anderson, 1988; Stahl & Kaumanns, 2003). Although feeding competition is arguably a disruptive event that puts social cohesion at risk, this is only part of the story. To preserve their social relationships, higher-ranking individuals have to make concessions to lower-ranking group members (de Waal, 1986). The latter may obtain some share of resources by exchanging various forms of

appeasement, conciliation, and reassurance behavior with partners of higher rank. There is a particularly high level of tolerance toward the subordinate when the social relationship between partners is valuable, with high-ranking individuals tolerating co-feeding from kin-related partners (Bélisle, Prud'homme, & Dubuc, 2012), coalition partners (Berman, Ionica, & Jinhua, 2007), and sexual partners (Dubuc, Hughes, Cascio, & Santos, 2012) more readily than from other individuals. Levels of social tolerance also vary between species. An example of this is the higher frequency of co-feeding in bonobos (*Pan paniscus*) than in chimpanzees (*Pan troglodytes*), which may be linked to different expectations about the acceptance of sharing in different societies (Amici, Call, & Aureli, 2012; Hare, Melis, Woods, Hastings, & Wrangham, 2007).

The genus *Macaca* is a suitable model to investigate whether balance of power and resource partitioning are related patterns that are embedded in the species-specific system of social relationships. Although all macaques live in multimale–multifemale groups with linear dominance hierarchies, they display wide interspecific variation in their social style. Macaque species can be ordered along a continuum from those characterized by rather strong social intolerance and steep gradient of dominance coupled with conspicuous submission signals to others displaying higher levels of tolerance and more balanced dominance relationships that leave room for negotiation (Balasubramaniam et al., 2012; Duboscq et al., 2017; Thierry, 2000, 2007). Conflicts in the more tolerant macaques involve a higher proportion of protests and counterattacks, and are more often followed by reconciliation between previous opponents. Studies have revealed that interspecific contrasts are associated with a suite of behavioral traits that travel together through the evolutionary process. Agonistic and dominance behavior covaries with such traits as degree of maternal permissiveness, amount of alloparental care, form of social play, degree of kin preference among females, diversity of communicative signals, and personality dimensions (Adams et al., 2015; Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Dobson, 2012; Petit, Bertrand, & Thierry, 2008; Scopa & Palagi, 2016; Thierry et al., 2008). There are also hints that in competitive situations, individuals from the more tolerant species can stay closer to each other more easily than their more intolerant counterparts, thus enabling more group members to access the same resources (Bélisle et al., 2012; de Waal & Luttrell, 1989; Matsumura, 2001; Petit, Desportes, & Thierry, 1992). However, no comparative study has been conducted so far to evaluate whether food partitioning is more equitable in tolerant macaques than in intolerant ones when incentives are clumped and defendable.

This study examines whether the degree of inequality in food distribution may be related to social style in two social groups that were maintained in similar semi-free ranging conditions to minimize the influence of environmental variation. The groups belonged to two different species characterized by contrasting styles of social relationships, namely rhesus macaques (*Macaca mulatta*), which display the high dominance asymmetry and strong nepotism typical of intolerant macaques, and Tonkean macaques (*Macaca tonkeana*), which exhibit the shallow dominance gradient and low kinship bias distinguishing the social style of tolerant macaques (Thierry, 2007). We conducted feeding trials where fresh food was distributed to group members under different clumping conditions. As the most appetizing food disappears first and animals become progressively satiated, levels of competition should decrease from the beginning to the end of the trials. This allowed us to test the following predictions: (1) higher-ranking individuals should have earlier access to food than lower-ranking counterparts, and this effect should be stronger in rhesus macaques than in Tonkean macaques; (2) a higher degree of spatial clumping should limit food access to low-ranking individuals, and this effect should be stronger in rhesus macaques than in Tonkean macaques; (3) the time spent by group members within the feeding area at the early stage of trials should be significantly longer in Tonkean macaques than in rhesus macaques, while an opposite trend should be found for rates of agonistic interactions.

2 | METHODS

2.1 | Subjects

We studied one group of rhesus macaques and one group of Tonkean macaques maintained at the Primate Center of the University of Strasbourg. Each group was semi-free ranging in a wooded enclosure of approximately 1 acre. The group of rhesus macaques had been founded 10 years before the study. At the beginning of the experiments, it contained one adult male and three matrilines composed of five adult females and their offspring: four subadult individuals (three males, one female), and two individuals under the age of three (two females). The group of Tonkean macaques had been founded 11 years before the study. At the start of experiments, it contained one adult male and two matrilines composed of six adult females and their offspring: four subadults (one male, three females), and four individuals under the age of 3 (three males, one female). Adults were defined as subjects at least 6 years old, and subadults as subjects aged 3–5 years (see Supporting information, Table S1). In both groups, the adult male was unrelated to other group members. Monkey dry commercial diet and water were available ad libitum in an indoor shelter. This diet was supplemented with fresh fruit and vegetables distributed once a week in the enclosure.

2.2 | Ethics statement

The research was carried out in accordance with the Guidelines for the use of animals in research of the Association for the Study of Animal Behaviour. All procedures complied with French laws. They were conducted under licence N°408 from the French Agricultural Department (manipulation of non-human primate social groups).

2.3 | Experimental procedure

Experiments were conducted between June 1988 and October 1989. At the time of the weekly distribution of fresh food, subjects received a mixture of banana, apple, and carrot pieces, with quantities based on one fruit or vegetable of each type per individual. The type and amount of food were the same as those normally distributed to animals outside

experimental periods. While food was spread across an area of approximately 6–12 m^2 during regular food supply, the extent of food distribution was tightly controlled during experiments (see below). A keeper carried the food into the enclosures in buckets and scattered it on the ground over an area delineated by a circle of powdered chalk. Bananas were more desirable than apples which, in turn, were more desirable than carrots (Belzung & Anderson, 1986). Consequently, subjects were expected to enter the feeding site as early as possible to obtain the most desirable food. The two observers, located ten meters from the area, started recording as soon as the food was distributed. One (C. Desportes) carried out scans at 1-min intervals, using check sheets to note all adult or subadult subjects present within the feeding area. Individuals with any part of their body on the line of the circle were considered to be inside the feeding area. The second observer (B. Thierry) recorded all occurrences of agonistic interactions (supplantations and conflicts) occurring between adult/subadults and involving at least one subject that was located within the feeding area. Each trial lasted half an hour. Note that scraps of apples and carrots remained on the ground at the end of trials, and were mainly constituted of tegument parts. There were three experimental conditions according to the diameter of the feeding area: small-clumped (1 m), medium-clumped (2 m), and large-clumped (4 m). We carried out four trials for each area condition, that is, twelve trials in random order for each group.

2.4 | Assessment of dominance relationships

The dominance status of individuals in each group was assessed using supplantations and unidirectional conflicts recorded during trials and nine 3-hr competition tests conducted during the same period around a source of fruit juice (see Thierry et al., 1994). Socprog 2.6 software (Whitehead, 2009) was then applied to the matrices built from these data to rank individuals in dominance hierarchies (de Vries, 1995, 1998), see supporting information, Table S1. For adult and subadult subjects, the linearity index *h'* was equal to .82 ($P = .001$) in rhesus macaques, and .64 ($P = .008$) in Tonkean macaques.

2.5 | Statistical analyses

We performed general linear mixed model (GLMM) analyses using *R 3.2.2* (R Core Team, 2015) and the package *lme4* (Bates, Maechler, Bolker, & Walker, 2014). Testing days and individual identities nested within age (adult, subadult) were random factors.

A first analysis addressed co-feeding through the presence of individuals in the feeding area. The trials were divided into three successive time periods of 10 min (first: 1–10 min, second: 11–20, third: 21–30). The target variable was the number of scans each subject was recorded in the area within a given time period. Predictor variables were species (rhesus macaque, Tonkean macaque), time period (first, second, third), clumped condition (small, medium, large), and dominance rank (1 to 10–11). As the study focused on interspecific contrasts in dominance style, we included the two ordered interactions between species and dominance rank in the model, with either time period or clumped condition as the third variable. We also included all interactions between two variables. Moreover, the sex variable was added to the model to test for a potential effect.

A second analysis addressed the agonistic interactions induced by feeding competition. The target variable was the number of interactions initiated by each subject within 10-min periods. Predictor variables were species, time period, and clumped condition. We investigated all statistical interactions between species and other variables (time period, clumped condition, sex). This analysis excluded dominance rank, as it is known that higher-ranking individuals come first in a context of feeding competition, making patterns of agonistic interactions dependent on the subjects' presence in the feeding area.

Target variables corresponded to count data, so we ran GLMM analyses using a Poisson distribution with a log link. Predictor variables showed no significant collinearity (variance inflation factor lower than 3 for all variables). Given that several predictor variables could influence target variables, we used an information-theoretic approach to evaluate candidate sets of models. After selecting the appropriate predictors, we tested different combinations (Burnham & Anderson, 2002). The use of second-order Akaike's Information Criterion (AICc) determined the level of support for each model, thus making it possible to carry out a model selection. The model with the lowest AICc value is often considered as the model that best fits the data, although any model within two AICc units of the lowest value is, by convention, considered to fit the data just as well (Burnham & Anderson 2002). We therefore calculated the RVI (Relative Variable Importance) for all predictor variables using the model.avg function of the *MuMIn* package (Barton 2016). This allowed us to choose the best-fitting model by retaining the model that was within two AICc units of the lowest value, and which only contained variables with an RVI of at least 0.7 (Burnham & Anderson 2002; Symonds & Moussalli 2011).

Once we had identified the best models, we performed post-hoc analyses to examine the interactions found in the GLMMs. For interactions between a quantitative and a qualitative variable, we ran post-hoc analyses on pairwise interaction contrasts using the testInteraction function in the *Phia R* package (de Rosario-Martinez, 2015). This method adjusts interaction *p* values with a Holm–Bonferonni correction, and removes the influences from the main effects in the model. For interactions between two qualitative variables, multiple pairwise comparisons using least squares means were run using the *lsmeans R* package with a Tukey's adjustment method (Lenth, 2014). We used an identical procedure to analyze interactions between two qualitative and one quantitative variables.

3 | RESULTS

3.1 | Presence in the feeding area

The best-fitting model was explained by species, time period, clumped condition, dominance rank, and interactions between these variables (Supporting information, Table S2: model 1). A post-hoc analysis of the interaction between species, time period, and dominance rank showed that Tonkean macaques spent more time on average in the feeding

area than rhesus macaques during the first period (9.1 ± 1.7 vs. 3.8 ± 3.4, $z = -8.7$, $p < .001$), but contrasts between species were not significant in the second (4.1 ± 3.1 vs. 3.7 ± 3.0, $z = -.66$, $p = .986$) and third periods (2.1 ± 3.0 vs. 2.6 ± 3.2, $z = 1.5$, $p = .694$) (Figure 1a). Tonkean macaques spent more time in the feeding area during the first 10-min period than during the second period (LSMeans post-hoc comparison test, 9.1 ± 1.7 vs. 4.1 ± 3.1, $z = 7.6$, $p < .001$) and the third period (9.1 ± 1.7 vs. 2.1 ± 2.9, $z = 21.6$, $p < .001$). They were also present in the area more often on average during the second period than the third (4.1 ± 3.1 vs. 2.1 ± 2.9, $z = 9.3$, $p < .001$) (Figure 1a). The low values of standard deviations relative to mean values in the first period indicated limited individual variation: more than half of subjects were present in 9 scans out of 10. In the second and third periods, higher standard deviations relative to mean values pointed to a higher variability regarding subjects' presence. Rhesus macaques spent on average less time in the area over the third period than during the first (2.6 ± 3.2 vs. 3.8 ± 3.4, $z = 3.4$, $p = .010$) and the second (2.6 ± 3.2 vs. 3.7 ± 3.0, $z = 5.8$, $p < .001$), but the difference between the first and the second periods was not statistically significant (3.8 ± 3.4 vs. 3.7 ± 3.0, $z = -2.4$, $p = .170$) (Figure 1a). The high values of standard deviations relative to mean values revealed wide variability regarding subjects' presence.

We then focused on dominance effects in each combination of species and period variables. This showed that the higher the dominance rank of rhesus macaques, the longer they stayed in the feeding area during the first period (LSMeans post-hoc comparison test, slope coefficient $\alpha = -.23$, $z = -10.3$, $p < .001$) (Figure 1b). A similar effect was found in Tonkean macaques, albeit weak, as indicated by the slope coefficient ($\alpha = -.04$, $z = -2.4$, $p = .021$). In both species, the lower the dominance rank of individuals, the longer they spent in the feeding area during the third period (rhesus: $\alpha = .17$, $z = 6.9$, $p < .001$; Tonkean: $\alpha = .094$, $z = 4.1$, $P < .001$) (Figure 1d). A similar trend appeared for the second period, but did not yield statistically significant effects (rhesus macaques: $\alpha = -.003$, $z = -.13$, $p = .896$; Tonkean macaques: $\alpha = .015$, $z = .75$, $p = .545$) (Figure 1c).

A second post-hoc analysis focused on the interaction between the species, clumped condition, and dominance rank variables. We did not find any significant contrasts in any clumped conditions within species (LSMeans post-hoc comparison test, rhesus macaques: small vs medium, 3.4 ± 3.5 & 3.3 ± 3.3, $z = -.003$, $p > .999$, medium vs. large 3.3 ± 3.3 & 3.5 ± 3.1, $z = -.52$, $p = .996$, small vs. large 3.4 ± 3.5 & 3.5 ± 3.1, $z = -.52$, $p = .996$, Tonkean macaques: small vs. medium 5.0 ± 4.1 & 5.3 ± 4.0, $z = -.24$, $p > .999$, medium vs. large 5.3 ± 4.0 & 5.0 ± 3.8, $z = 1.0$, $p = .920$, 5.0 ± 4.1 & 5.0 ± 3.8 small vs. large $z = .76$, $p = .974$), and between species (small: rhesus vs. Tonkean 3.4 ± 3.5 & 5.0 ± 4.1, $z = -2.4$, $p = .173$, medium: rhesus vs. Tonkean 3.3 ± 3.3 & 5.3 ± 4.0, $z = -2.6$, $p = .110$, large: rhesus vs. Tonkean 3.5 ± 3.1 & 5.0 ± 3.8, $z = -1.3$, $p = .776$) (Figure 2a). We then focused on dominance effects in each combination of species and clumped conditions. The higher the rank of rhesus macaques, the longer they stayed in the small-clumped feeding area (LSMeans post-hoc comparison test, $\alpha = -.083$, $z = -3.8$, $p < .001$), but this was not true for the medium- ($\alpha = -.006$, $z = -.28$, $p = .783$) and the large-clumped areas ($\alpha = .024$, $z = 1.1$, $p = .393$) (Figure 2b–d). No significant influence of clumped conditions was found for Tonkean macaques (small: $\alpha = .022$, $z = 1.2$, $p = .39$, medium: $\alpha = .030$, $z = 1.6$, $p = .346$, large: $\alpha = .014$, $z = .71$, $p = .575$) (Figure 2b–d).

3.2 | Agonistic interactions

The best-fitting model was explained by species, time period and the interaction between these two variables (Supporting information, Table S3: model 4). A post-hoc analysis of this interaction showed that Tonkean macaques initiated more agonistic interactions in the feeding area during the first period than the second (LSMeans post-hoc comparison test, .48 ± .70 vs. .13 ± .44, $z = 5.1$, $p < .001$) and third

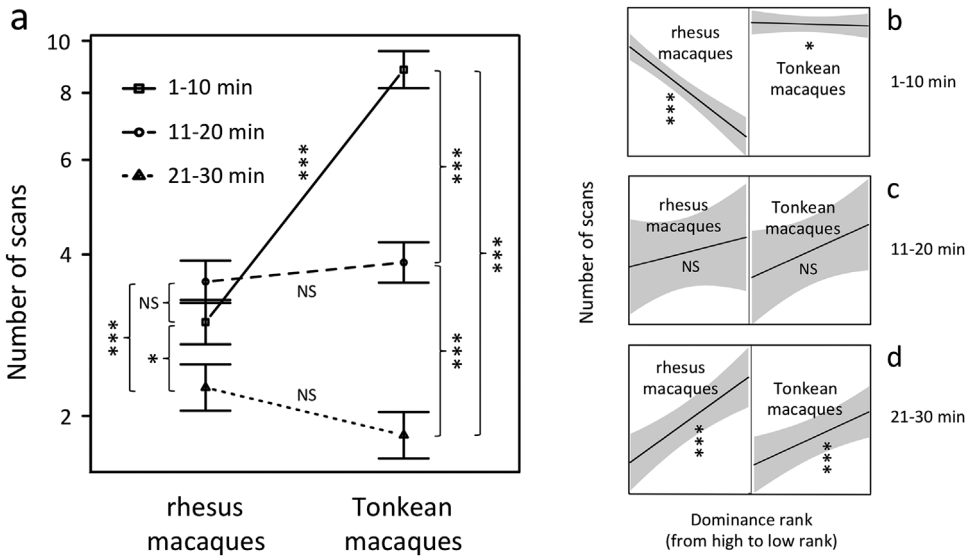

FIGURE 1 Effect of species and dominance rank on presence in the feeding area according to time periods (first, second, and third 10-min periods)

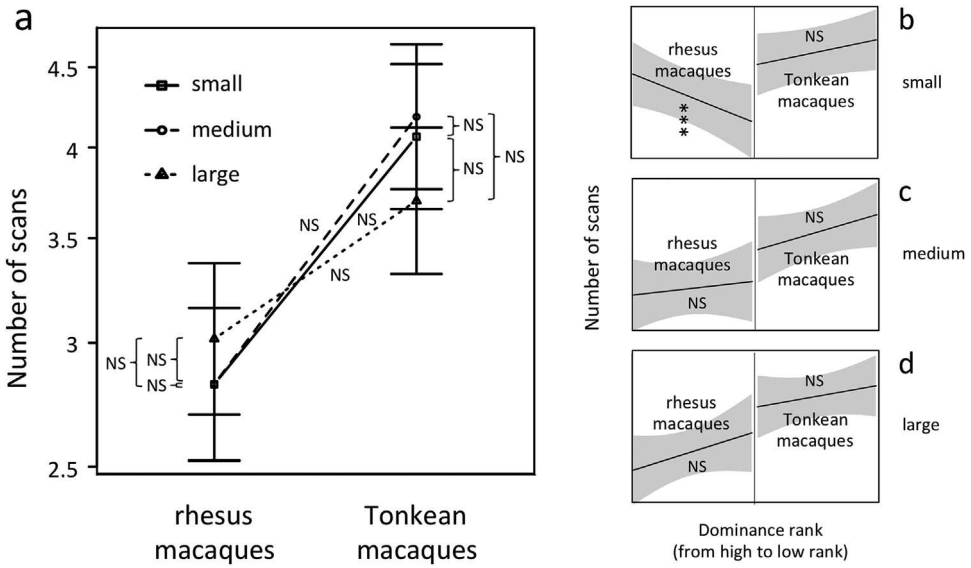

FIGURE 2 Effect of species and dominance rank on presence in the feeding area according to clumped conditions (small, medium, and large)

periods (.48 ± .70 vs. .015 ± .12, $z = 5.0$, $p < .001$), and also initiated more interactions during the second period than the third (.13 ± .44 vs. .015 ± .12, $z = 3.0$, $p = .034$) (Figure 3). Rhesus macaques had less numerous agonistic interactions over the third period than during the two previous periods (third vs. first: .38 ± .90 vs. 1.1 ± 1.6, $z = 6.0$, $p < .001$, third vs. second: .38 ± .90 vs. .83 ± 1.7, $z = 4.5$, $p < .001$), but no statistically significant difference appeared between the first and second periods (1.1 ± 1.6 vs. .83 ± 1.7, $z = 1.8$, $p = .451$) (Figure 3). Interspecific contrasts showed that rhesus macaques initiated more agonistic interactions than Tonkean macaques during the third period (.83 ± 1.7 vs. .13 ± .44, $z = 3.3$, $p = .015$), but contrasts did not yield significant differences for the two previous periods (first .38 ± .90 vs. .02 ± .12, $z = .77$, $p = .973$, second: 1.1 ± 1.6 vs. .48 ± .70, $z = 1.8$, $p = .450$) (Figure 3).

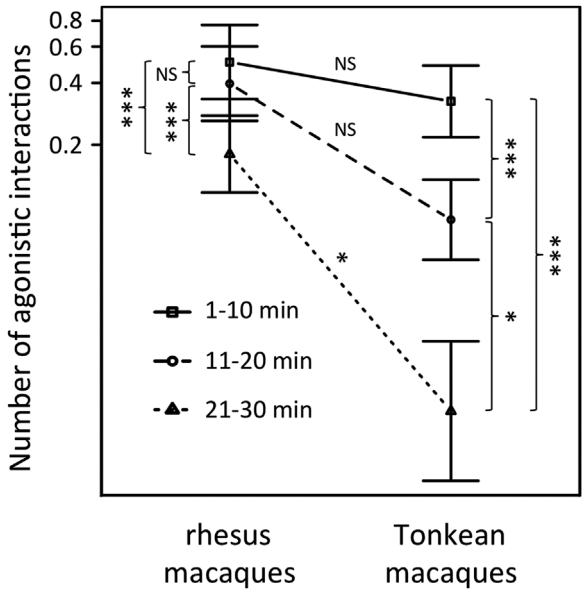

FIGURE 3 Effect of species and time period (first, second, and third 10-min periods) on the number of agonistic interactions

4 | DISCUSSION

Distributing food in a limited area induced contrasting responses to competition in groups of rhesus and Tonkean macaques. In the former, social hierarchy regulated access to resources, as classically reported in this species and other intolerant macaques (Bélisle et al., 2012; Belzung & Anderson, 1986; Brennan & Anderson, 1988; Furuichi, 1983; Peláez, Gil-Burmann, & Sánchez, 2000). Dominant individuals had priority of access to food: the higher the rank of rhesus macaques, the longer they stayed in the feeding area in the first trial period, while the lower their rank, the longer they stayed in the feeding area during the third period. We found similar but weaker trends in Tonkean macaques. In the first period in particular, most group members were present, meaning that they could eat simultaneously when the most desirable food was still available. Time spent co-feeding varied little between individuals according to dominance rank, indicating that food partitioning was relatively equal among group members. Such results could be predicted from the social style reported in each species. Whereas social tension and conflicts of interests are mainly ruled by hierarchical means in rhesus macaques (de Waal & Luttrell, 1985; Maestripieri, 2007), Tonkean macaques have various forms of conciliatory behavior at their disposal to manage them (Demaria & Thierry, 2001; Petit et al., 1992; Thierry, 1984; Thierry, Demaria, Preuschoft, & Desportes, 1989).

The degree of resource concentration generally affects the intensity of competition between conspecifics, as it determines whether resources are likely to be protected from certain individuals by others (Belzung & Anderson, 1986; Chancellor & Isbell, 2008; Janson & van Schaik, 1988; Stahl & Kaumanns, 2003). The present study, however, did not identify any significant differences between

species in the time spent in food area according to the degree of spatial clumping. It is likely that the food distribution was concentrated enough to create direct competition among group members, even in the more dispersed condition. However, the higher the dominance rank of rhesus macaques, the longer they stayed in the small-clumped feeding area, which showed that lower-ranking individuals had diminished access to food when inter-individual distances around fruit were reduced. This rank effect did not occur in Tonkean macaques, where subordinates can display more assertiveness toward higher-ranking individuals than in more intolerant macaques, allowing them to feed at shorter distances from each other (Bélisle et al., 2012; Petit et al., 1992; Thierry, 2000). They were able to eat together even when the feeding area was no more than 1-m wide, typically shoulder-to-shoulder around the pile of food.

As expected, we found broad cross-species contrasts in the pattern of inter-individual contests. The frequencies of agonistic interactions steadily decreased in Tonkean macaques from the first to the last period of trials, which has to be considered alongside evidence that the time spent by group members in the feeding area decreased along the same schedule, meaning that individuals were less numerous around the food as time progressed. Frequencies of agonistic interactions were similar in Tonkean and rhesus macaques during the first period, even if the number of subjects present in the feeding area were much larger in the former. Rhesus macaques exhibited high levels of agonism during all periods, and especially during the first and second periods. Threats and supplantations are commonly used by higher-ranking individuals to exclude lower-ranking group members from proximity to food; the latter have to wait for the former to leave the foraging area. This explains the succession pattern reported in intolerant macaques, where dominant individuals have an earlier access to food, followed by intermediate-ranking subjects then subordinates, and accounts for the sustained levels of agonism throughout trials (Belzung & Anderson, 1986).

A main conclusion of this study is that Tonkean macaques were able to feed together on a spatially restricted patch despite competition, while rhesus macaques regulated access to resources through dominance-driven behavior, thus limiting the occurrence of co-feeding. As an outcome, food resources were more equitably distributed among group members in tolerant macaques than in their intolerant counterparts. It has already been established that macaque species differ in the steepness of the dominance gradient and degree of social tolerance between conspecifics (Balasubramaniam et al., 2012; Duboscq et al., 2017; Thierry, 2007). The present study adds that resource partitioning also covaries with these patterns. It should be emphasized that the probability of lower-ranking individuals protesting against the claims made by higher-ranking individuals on goods and services is higher in tolerant macaques, which means that the outcome of competitive interactions is more negotiable than in their more intolerant counterparts (Amici et al., 2012; Bélisle et al., 2012; Dobson, 2012; Thierry, 2007). When two group members compete for a resource, they not only have to take into account the costs of aggression and the gains brought by the resource, but also the value of their relationship (de Waal, 1986). In such a perspective, dominance gradient and social tolerance represent two aspects of the same phenomenon. Environmental factors likely influence the balance of power between partners in all animal societies (Mattison et al., 2016; Vehrencamp, 1983; Watts, 2010). It should be noted, however, that no consistent relationships have been found so far between variations in social style and ecological parameters in macaques and other non-human primates (Clutton-Brock & Janson, 2012; Thierry, 2007, 2008).

The present work was conducted in two groups of macaques kept in semi-free ranging conditions. Future research in additional populations should seek to confirm the occurrence of interspecific contrasts in co-feeding patterns among primates, and extend our knowledge of the link between social style and resource partitioning in the natural environment.

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REFERENCES

Adams, M. J., Majolo, B., Ostner, J., De Marco, A., Thierry, B., Engelhardt, A., & Weiss, A. (2015). Personality structure and social style in macaques. *Journal of Personality and Social Psychology*, *109*, 338–353. https://doi.org/10.1037/pspp0000041

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, *5*, 326–383. https://doi.org/10.1146/annurev.es.05.110174.001545

Amici, F., Call, J., & Aureli, F. (2012). Aversion to violation of expectations of food distribution: The role of social tolerance and relative dominance in seven primate species. *Behaviour*, *149*, 345–368. https://doi.org/10.1163/156853912×637833

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., & de Waal, F. B. M. (2012). Hierarchical steepness and phylogenetic models: Phylogenetic signals in Macaca. *Animal Behaviour*, *83*, 1207–1218. https://doi.org/10.1016/j.anbehav.2012.02.012

Barton, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6 Available at: https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). Lme4: Linear mixed-effects models using Eigen and S4. *R Package Version*, *1* (7). Available at: https://CRAN.R-project.org/packages=lme4

Bélisle, P., Prud'homme, B., & Dubuc, C. (2012). The impact of kinship, defence cost and priority of access on food competition. In J. B. Leca, M. A. Huffman, & P. L. Vasey (Eds.), *The monkeys of Stormy Mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 331–355). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139019415.026

Belzung, C., & Anderson, J. R. (1986). Social rank and responses to feeding competition in rhesus monkeys. *Behavioural Processes*, *12*, 307–316. https://doi.org/10.1016/0376-6357(86)90001-X

Berman, C. M., Ionica, C., & Jinhua, L. (2007). Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China. *Behaviour*, *144*, 631–661. https://doi.org/10.1163/156853907781347790

Boccia, M. L., Laudenslager, M., & Reite, M. (1988). Food distribution, dominance, and aggressive behaviors in bonnet macaques. *American Journal of Primatology*, *16*, 123–130. https://doi.org/10.1002/ajp.1350160203

Brennan, J., & Anderson, J. R. (1988). Varying responses to feeding competition in a group of rhesus monkeys (*Macaca mulatta*). *Primates*, *29*, 353–360. https://doi.org/10.1007/BF02380958

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer Science & Business Media.

Chancellor, R. L., & Isbell, L. A. (2008). Punishment and competition over food in captive rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, *75*, 1939–1947. https://doi.org/10.1007/b97636

Chapais, B. (1991). Primates and the origins of aggression, power, and politics among humans. In J. D. Loy, & C. B. Peters (Eds.), *Understanding behavior: What primate studies tell us about human behavior* (pp. 190–228). New York, NY: Oxford University Press.

Ciani, F., Dall'Olio, S., Stanyon, R., & Palagi, E. (2012). Social tolerance and adult play in macaque societies: A comparison with different human cultures. *Animal Behaviour*, *84*, 1313–1322. https://doi.org/10.1016/j.anbehav.2012.09.002

Clutton-Brock, T., & Janson, C. (2012). Primate socioecology at the crossroads: Past, present, and future. *Evolutionary Anthropology*, *21*, 136–150. https://doi.org/10.1002/evan.21316

de Rosario-Martinez, H. (2015). Phia: Post-Hoc InteractionAnalysis. *R package version 0.2-1*. Available at: https://CRAN.R-project.org/package=phia

de Waal, F. B. M. (1984). Coping with social tension: Sex differences in the effect of food provision to small rhesus monkey groups. *Animal Behaviour*, *32*, 765–773. https://doi.org/10.1016/S0003-3472(84)80152-9

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, *50*, 1375–1389. https://doi.org/10.1016/0003-3472(95)80053-0

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Animal Behaviour*, *55*, 827–843. https://doi.org/10.1006/anbe.1997.0708

de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *Quarterly Review of Biology*, *61*, 459–479. https://doi.org/10.1086/415144

de Waal, F. B. M., & Luttrell, L. M. (1985). The formal hierarchy of rhesus macaques: An investigation of the bared-teeth display. *American Journal of Primatology*, *9*, 73–85. https://doi.org/10.1002/ajp.1350090202

de Waal, F. B. M., & Luttrell, L. M. (1989). Toward a comparative socioecology of the *genus Macaca*: Different dominance styles in rhesus and stumptailed macaques. *American Journal of Primatology*, *19*, 83–109. https://doi.org/10.1002/ajp.1350190203

Demaria, C., & Thierry, B. (2001). A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour*, *138*, 397–410. https://doi.org/10.1163/15685390152032514

Dobson, S. D. (2012). Coevolution of facial expression and social tolerance in macaques. *American Journal of Primatology*, *74*, 229–235. https://doi.org/10.1002/ajp.21991

Duboscq, J., Neumann, C., Agil, M., Perwitasari-Farajallah, D., Thierry, B., & Engelhardt, A. (2017). Degrees of freedom in social bonds of crested macaque females. *Animal Behaviour*, *123*, 411–426. https://doi.org/10.1016/j.anbehav.2016.11.010

Dubuc, C., Hughes, K. D., Cascio, J., & Santos, L. R. (2012). Social tolerance in a despotic primate: Co-feeding between consortship partners in rhesus macaques. *American Journal of Physical Anthropology*, *148*, 73–80. https://doi.org/10.1002/ajpa.22043

Furuichi, T. (1983). Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates*, *24*, 445–455. https://doi.org/10.1007/BF02381678

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, *17*, 619–623. https://doi.org/10.1016/j.cub.2007.02.040

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*, 143–155. https://doi.org/10.1093/beheco/2.2.143

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour*, *105*, 165–185. https://doi.org/10.1163/156853988 × 00502

Kurtz, D. V. (2001). *Political anthropology: paradigms and power*. Boulder, CO: Westview Press.

Lenth, R. V. (2014). lsmeans: Least-squares means. *R package version 2.13*. Available at: https://CRAN.R-project.org/package=lsmeans

Maestripieri, D. (2007). *How rhesus macaques and humans have conquered the world*. Chicago, IL: University of Chicago Press. https://doi.org/10.7208/chicago/9780226501215.001.0001

Majolo, B., de Bortoli Vizioli, A., & Schino, G. (2008). Costs and benefits of group living in primates: Group size effects on behaviour and demography. *Animal Behaviour*, *76*, 1235–1247. https://doi.org/10.1016/j.anbehav.2008.06.008

Matsumura, S. (2001). The myth of despotism and nepotism: Dominance and kinship in matrilineal societies of macaques. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 441–462). Tokyo: Springer. https://doi.org/10.1007/978-4-431-09423-4_22

Mattison, S. M., Smith, E. A., Shenk, M. K., & Cochrane, E. E. (2016). The evolution of inequality. *Evolutionary Anthropology*, *25*, 184–199. https://doi.org/10.1002/evan.21491

Nakagawa, N. (1990). Choice of food patches by Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology*, *21*, 17–29. https://doi.org/10.1002/ajp.1350210103

Peláez, F., Gil-Burmann, C., & Sánchez, S. (2000). Feeding tactics in juvenile rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology*, *51*, 147–152. https://doi.org/10.1002/(SICI)1098-2345(200006)51:2%3C147::AID-AJP4%3 E3.0.CO;2-L

Petit, O., Bertrand, F., & Thierry, B. (2008). Social play in crested and Japanese macaques: Testing the covariation hypothesis. *Developmental Psychobiology*, *50*, 399–407. https://doi.org/10.1002/dev.20305

Petit, O., Desportes, C., & Thierry, B. (1992). Differential probability of "coproduction" in two species of macaque (*Macaca tonkeana*, *M. mulatta*). *Ethology*, *90*, 107–120. https://doi.org/10.1111/j.1439-0310. 1992.tb00825.x

R Core Team (2015). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. Available at: https://www.R-project.org

Scopa, C., & Palagi, E. (2016). Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). *Journal of Comparative Psychology*, *130*, 153–161. https://doi.org/10.1037/com0000028

Southwick, C. H. (1967). An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). *Behaviour*, *28*, 182–208. https://doi.org/10.1163/156853967×00235

Stahl, D., & Kaumanns, W. (2003). Food competition in captive female sooty mangabeys (*Cercocebus torquatus atys*). *Primates*, *44*, 203–216. https://doi.org/10.1007/s10329-002-0012-x

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*, 291–309. https://doi.org/10.1007/s002650050390

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*, 13–21. https://doi.org/10.1007/s00265-010- 1037-6

Thierry, B. (1984). Clasping behaviour in *Macaca tonkeana*. *Behaviour*, *89*, 1–28. https://doi.org/10.1163/156853984×00010

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C., & Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In J. J. Roeder, B. Thierry, J. R. Anderson, & N.

Herrenschmidt (Eds.), *Current primatology, Vol. 2: Social development, learning and behaviour* (pp. 103–117). Strasbourg: Université Louis Pasteur.

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 106–128). Berkeley, CA: University of California Press.

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology*, *16*, 224–238. https://doi.org/10.1002/evan.20147

Thierry, B. (2008). Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology*, *17*, 93–96. https://doi.org/10.1002/evan.20168

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A comparative study of conflict resolution in macaques: Insights into the nature of trait covariation. *Animal Behaviour*, *75*, 847–860. https://doi.org/10.1016/j.anbehav. 2007.07.006

Thierry, B., Demaria, C., Preuschoft, S., & Desportes, C. (1989). Structural convergence between silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia Primatologica*, *52*, 178–184. https://doi.org/10.1159/000156396

Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, *31*, 667–682. https://doi.org/10.1016/S0003-3472(83)80222-X

Watts, D. P. (2010). Dominance, power, and politics in nonhuman and human primates. In P. M. Kappeler, & J. B. Silk (Eds.), *Mind the gap* (pp. 109–138). Berlin: Springer. https://doi.org/10.1007/978-3-642-02725-3_5

Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765–778. https://doi.org/10.1007/s00265-008-0697-y

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Female mate choice and male–male competition in Tonkean macaques: Who decides?

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Abstract

The theory of sexual selection predicts that females should be discriminatory in the choice of sexual partners. Females can express their choice in two ways. In direct mate choice, they show preferences for certain partners. In indirect mate choice, they select partners by displaying sexually attractive traits, thus eliciting contest competition between males. We focused on a primate species in which females advertise the timing of their ovulation and studied the balance between these two choice strategies. We tested predictions related to three hypotheses about direct and indirect female choice, namely the best-male, graded-signal and weak-selectivity hypotheses. We investigated the sexual and agonistic interactions occurring during oestrous periods in five captive groups of Tonkean macaques (*Macaca tonkeana*). The results showed that dominant males used mate guarding to monopolise sexual access to parous females that were in the fertile stage of their reproductive cycle, while lower-ranking males monitored only nulliparous females. The distribution of sexual presentations indicated that females accepted different types of partners, supporting the weak-selectivity hypothesis regarding direct mate choice. The analysis of behavioural sequences revealed that mate-guarding males used mild coercive behaviours to prevent females from mating with other males at conception time. The distribution of mounts showed that females mainly mated with dominant males, which leads us to argue that the best-male hypothesis provides the most parsimonious explanation regarding indirect mate choice in Tonkean macaques. At the individual level, it may be concluded that male competitive strategies prevented females from exercising direct mate choice. At the evolutionary level, however, female sexual advertising and thus indirect choice promoted competition between males. The outcome is that indirect mate choice appears more important than direct mate choice in female Tonkean macaques.

KEYWORDS

direct mate choice, indirect mate choice, mate guarding, sexual coercion, primate, *Macaca tonkeana*

1 | INTRODUCTION

A number of reasons may incite females to be discriminatory in their choice of sexual partners. They can select males who will provide benefits in terms of resources, protection or paternal care and can also favour males displaying a phenotype that is beneficial for the genetic quality of their offspring (Andersson, 1994; Clutton-Brock, 2009; Setchell & Kappeler, 2003). Females express their choices in either a direct or indirect way. In direct mate choice, they exhibit preferences by showing different responses to potential mates, thus affecting

the mating chances of the latter. Females may behave proceptively by soliciting copulation from certain males and may also display various levels of receptivity according to partners, accepting the sexual advances made by one while rejecting those of another. In indirect mate choice, females select the best competitors by eliciting contest competition between males. They can achieve this by spatial clumping, synchronised reproduction or announcing their fertility through specific behavioural and morphological cues (Manson, 2010; Wiley & Poston, 1996). Although direct and indirect mate choices represent two different strategies, they may co-occur in the same species. In elephant seals (*Mirounga angustirostris*) and chacma baboons (*Papio ursinus*), for example, fertile females both exhibit preferences for some males and advertise their reproductive state or even their copulations (Clarke, Henzi, & Barrett, 2009; Cox & Le Boeuf, 1977; O'Connell & Cowlishaw, 1994). It should be emphasised that indirect mate choice is not less specific than direct mate choice and could even permit a more reliable assessment of mates (Wiley & Poston, 1996). Whether or not direct and indirect mate choices could be equally developed or related through some trade-off at the species level remains an open question.

Mate choice is expected to be especially important when female reproductive costs are elevated. This should be particularly true for animals such as primates, in which low reproductive rates are related to extended periods of gestation, lactation and raising offspring. High dominance status is a main predictor of male reproductive success in group-living primates, and females might select dominant males because they provide protection and access to resources and possibly sire better offspring (Cowlishaw & Dunbar, 1991; Georgiev, Muehlenbein, Prall, Emery Thompson, & Maestripieri, 2015; Manson, 2010; Setchell & Kappeler, 2003; Small, 1989). In primate species where females display a prominent swelling of the anogenital skin that reaches maximal size around ovulation time, the "best-male hypothesis" states that such sexual swellings are honest signals of female fertility which incite male–male competition (Clutton-Brock & Harvey, 1976; Dixson, 1983). However, female primates are notably promiscuous and typically seek mating opportunities with different males during the same conceptive cycle; their criteria for mate preference remain unclear in many species: it could be that they are weakly selective (Kappeler & van Schaik, 2004; Manson, 2010; Setchell & Kappeler, 2003; Small, 1989). In species where infanticides occur, multiple mating by female primates is generally considered as a strategy aiming to confuse males about their paternity and so prevent infant killing by putative fathers (Hrdy, 1979; van Noordwijk & van Schaik, 2000).

It has been proposed that female partner preferences can change according to the period of their reproductive cycle: the females are expected to mate promiscuously in a first stage of sexual receptivity to dilute the chances of paternity among males, and then they should become more discriminative when the probability of ovulation increases, favouring mating with the dominant male to concentrate paternity on the individual that is the most capable of protecting their offspring (Zinner, van Schaik, Nunn, & Kappeler, 2004). According to the "graded-signal hypothesis," exaggerated swellings function as probabilistic signals of fertility; the initial stage with incomplete swelling aims to confuse multiple males about their possible paternity, while mating at the time of maximal swelling ensures paternity for the dominant male (Nunn, 1999; Street, Cross, & Brown, 2016; Zinner et al., 2004). In wild black capuchins (*Sapajus nigritus*), where females lack morphological signals of fertility, it was argued that their proceptive behaviours—and thus direct mate choice—also exhibit variations consistent with the graded-signal hypothesis (Tiddi, Wheeler, & Heistermann, 2015). Likewise, the best-male hypothesis was initially devised to account for indirect mate choice, but it may also be applied to female direct mate choice as females are frequently assumed to select the best male competitors as reproductive partners (Georgiev et al., 2015; Manson, 2010; Setchell & Kappeler, 2003).

The occurrence of intersexual conflict is another potent force driving the behaviour of individuals, and a main question in many species is to know whether the mating skew in favour of dominant males results from female choice for competitive males, or from the ability of the best competitors to exclude rivals from reproduction (Wong & Candolin, 2005). The diverging interests of the two sexes make it difficult to predict the outcome of the interaction between male and female reproductive strategies (Hunt, Breuker, Sadowski, & Moore, 2009; Stumpf, Martinez-Mota, Milich, Righini, & Shattuck, 2011). For instance, higher-ranking males may employ sexual coercion of females, using threats and attacks to prevent them from expressing possible preferences for rivals, and thus reinforce their own reproductive success (Muller & Wrangham, 2009; van Schaik, Pradhan, & van Noordwijk, 2004; Smuts & Smuts, 1993). While experimental pair-choice tests in long-tailed macaques (*Macaca fascicularis)* showed that females distributed their mating choices evenly across males, regardless of their dominance status (Nikitopoulos, Heistermann, de Vries, van Hooff, & Sterck, 2005), in situ studies of the same species found that almost all infants were sired by the first- and second-ranking males, indicating that male–male competition was a determinant factor (Engelhardt, Heistermann, Hodges, Nürnberg, & Niemitz, 2006; de Ruiter, van Hooff, & Scheffrahn, 1994).

A further factor affecting the interaction between female mate choice and male–male competition is the operational sex ratio, that is, the number of fertilisable females relative to the number of sexually active males (Cowlishaw & Dunbar, 1991; Emlen & Oring, 1977). When several females cycle synchronously in groups containing multiple males and females, none of the males can monopolise reproduction. They therefore compete for access to females, mainly through scramble competition: this is observed in seasonally breeding macaques, where most females associate and copulate opportunistically, shifting from one sexual partner to another, and thus allowing a significant proportion of males to obtain a share of paternity (Manson, 2010; Soltis, 2004). By contrast, when only one female is in oestrus at any one time—which is the case in year-round macaque breeders—a single male can guard the female throughout the fertile period, preventing rivals from gaining reproductive access (Paul, 2004; Soltis, 2004). As posited by the priority-of-access model (Altmann, 1962), dominance rank functions as a queue for mating success, whereby higher-ranking males have preferential access to fertile females. This leads to high reproductive skew through contest competition. To jump the queue and obtain mating opportunities, lower-ranking males must rely on

alternative tactics such as mating surreptitiously and forming coalitions to displace the mate-guarding male (Setchell & Kappeler, 2003; Soltis, 2004). When females honestly advertise their fertile state in the context of male–male contest competition, this should raise the stakes for mate guarding and thereby limit the opportunity for females to express sexual preferences, meaning that indirect mate choice could outweigh direct mate choice.

To investigate the balance between direct and indirect female mate choice in the context of mate guarding, we studied several captive groups of Tonkean macaques (*Macaca tonkeana*). This species originates from the island of Sulawesi, Indonesia, and lives in multimale–multifemale groups. Tonkean macaques are among the most tolerant species of the genus *Macaca* as indicated by several behavioural indices: in comparison with other macaques (Thierry, 2007), their social style is characterised by a shallow dominance gradient, that is, weak power differentials among individuals, and a high propensity to regulate social tension through multiple affiliative behaviours, frequent reconciliations and peaceful interventions in conflicts (De Marco, Cozzolino, Dessì-Fulgheri, & Thierry, 2011a; De Marco, Sanna, Cozzolino, & Thierry, 2014; Demaria & Thierry, 2001; Petit & Thierry, 1994). Reproduction occurs all year round, and sexual dimorphism is marked (Sanna, De Marco, Thierry, & Cozzolino, 2015). When females become sexually receptive, they attract males by displaying reliable signals of fertility: they repeatedly utter specific oestrous calls and exhibit a progressive pink-coloured swelling of the anogenital region that culminates in size around ovulation time. This prompts one of the males to guard the female, following and mounting her during a period of maximal swelling that averages 5–10 days and ceases at the end of the periovulatory phase (Aujard, Heistermann, Thierry, & Hodges, 1998; Thierry, Heistermann, Aujard, & Hodges, 1996).

In a first analysis, we tested the consistency of female direct and indirect choices by investigating the behaviour of the mate-guarding male. If the female displays selective attraction (direct choice) to the male selected by male–male competition (indirect choice), the mate-guarding male does not need to prevent the fertile female from interacting with other males, and he should mainly aim to exclude other males from interacting with her. In a second analysis, we tested three hypotheses regarding female choice by investigating female sexual presentations and matings: (i) best-male hypothesis: at the time of maximal swelling, females show exclusive preference for the highest-ranking male; (ii) weak-selectivity hypothesis: at the time of maximal swelling, females do not show any preference for particular males; (iii) graded-signal hypothesis: at the time of maximal swelling, females show exclusive preference for the highest-ranking male, and in the period preceding maximal swelling, they do not show any preference for particular males.

2 | METHODS

2.1 | Subjects

The observations were carried out on five groups of Tonkean macaques (B, C, D, E, F: see Table 1). They belonged to a population

TABLE 1 Information about groups and subjects

Group[a]	Origin of groups	Group composition	Name, parity[b] and age in years of focal females	Name and age in years of male partners
B	Founded in 1978 from the division in groups A and B of the original stock imported in 1972	11 mature[c] females, three mature males, six to 12 immature individuals	Ver (m, 24), Jul (m, 14), Mar (m, 13), Veo (m, 13), Bea (m, 10), Eri (n, 5), Els (n, 5), Dai (n, 5)	Nem (17), Vla (6), Bul (5)
C	Founded in 2005 from individuals removed from group B	Four mature females, four mature males, four to seven immature individuals	Pas (m, 12), Pam (n, 7), Pap (n, 5)	Nab (14), Pla (12), Pal (8), Soq (5)
D	Founded in 2007 from individuals removed from group A	Six mature females, seven mature males, five immature individuals	Gui (m, 18), Dan (p, 10)	Gre (19), Ach (13), Cha (11), Don (10), Gra (7), Cou (5), Dat (5)
E	Founded in 2007 from individuals removed from group B	Three mature females, four mature males, six to seven immature individuals	Sib (m, 10), Tet (m, 9)	Rim (11), Sho (10), Sim (10), Utt (8)
F	Founded in 2009 from individuals removed from group C	Two mature females, two mature males, three immature individuals	Nin (n, 8)	Nat (14), Nim (6)

[a]All subjects were captive bred except the oldest female (Ver) who was born in the wild and imported as a juvenile.
[b]Parity: n, nulliparous, p: primiparous, m: multiparous.
[c]Mature individuals were subjects at least 5 years of age.

originating from a stock imported to France in 1972 and were divided into groups A and B in 1978 (Herrenschmidt, 1977; Thierry, Anderson, Demaria, Desportes, & Petit, 1994). Group B lived in a 1-ha wooded park at the Centre de Primatologie in Strasbourg, France. The other four groups (C, D, E and F) stemmed from groups A and B (Table 1) and were housed in enclosures approx. 500 m^2 and 5 m high at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy (De Marco et al., 2014). Enclosures were furnished with wooden structures and perches. Commercial monkey diet pellets and fresh fruit and vegetables were provided to the animals outside observation hours. Water was available ad libitum. Our study adhered to all the legal requirements and guidelines of the Italian and French governments and followed ASAB/ABS guidelines for the treatment of animals in behavioural research.

2.2 | Observational methods

We conducted observations between 10:00 and 13:00 hr, from May 1994 to November 1995 in the Strasbourg group, and from June 2013 to May 2014 in the Rieti groups. We distinguished between three periods corresponding to different female reproductive states: (i) *anoestrous period*: days when the female did not present any genital swelling; (ii) *non-mate-guarding period*: oestrous days when a female displayed a genital swelling but was not followed by any males; (iii) *mate-guarding period*: oestrous days when a female displayed genital swelling and was followed by a male performing mate guarding (Figure 1). Mate-guarding days were defined as days when the same male was recorded following the same moving female while remaining within a distance of five metres at least nine times per 3-hr observation period (Aujard et al., 1998).

Focal subjects were 16 females over the age of five across the five groups (n = 8, 3, 2, 2, 1). We observed each of them continuously for 3 hr each morning, totalling a mean per female of 30 ± *SD* 8.7 hr during the anoestrous period, 16.8 ± 7.5 hr during the non-mate-guarding period and 26.7 ± 12.6 hr during the mate-guarding period. This represented a mean per female of 1.5 ± 0.6 ovarian cycles.

We used focal animal sampling (Altmann, 1974) to score interactions involving focal females and males over the age of five. These interactions are defined as followed: in both sexes, *approach* (moving to within 2 m of partner), *departure* (moving further than 2 m away from a partner) and *affiliation* (clasp, lipsmack, silent bared-teeth display); in females, *sexual presentation* (raising or directing the hindquarters towards a male); in males, *interposition* (the mate-guarding male places himself between a female and another male if either approaches the other), *sexual interest* (genital inspection [a male closely looks at, smells or touches a female anogenital region] and/or sexual solicitation [a male pushes or grasps the pelvic region of a female to raise or direct it towards himself]), and *mount* (note that Tonkean macaques are multimount ejaculators, meaning that not every mount ended in ejaculation).

We used instantaneous sampling (Altmann, 1974) at 10-min intervals to score social grooming, passive contact and proximity within a 2-m range between focal females and males. We also recorded conflicts (agonistic interactions involving physical aggression and/or vocal and visual threats) using all occurrence sampling (Altmann, 1974).

FIGURE 1 A mate-guarding male stays close to a swollen female while monitoring a rival on his left. Photograph: B. Thierry, Centre de Primatologie, Strasbourg

Five different observers were involved in the study (Strasbourg group B: F. Aujard, B. Thierry; Rieti groups C, D, E, F: A. De Marco, A. Sanna, E. Vero). As the Strasbourg and Rieti groups were sampled at different times, we could not measure interobserver reliability between all observers. However, use of the Cohen method (Cohen, 1960) showed that data from Rieti and Strasbourg observers consistently yielded interobserver reliability kappa coefficient values of over .65.

2.3 | Assessment of kinship and dominance relations

The coefficient of maternal relatedness was computed from pedigree data for each male/female dyad (median for all dyads: 0.0313, quartiles: 0, 0.156). The dominance status of individuals was assessed in each group using unidirectional conflicts and supplantations recorded during drinking competition tests (see Thierry et al., 1994). We applied SOCPROG software (Whitehead, 2009) to matrices built from these data to rank individuals in group dominance hierarchies (linearity index h', group B: 0.60; group C: 0.85; group D: 0.75; group E: 0.71; group F: 0.91). This allowed us to identify the top-ranking male in each group, that is, the highest male in the dominance hierarchy.

2.4 | Data processing

To estimate the strength of social bonds between the focal female and each male, we used a composite proximity index *Ip* based on proximity between partners during the anoestrous period. It was calculated from the formula $Ip = 2T_{0\,m} + 1/3T_{2\,m}$, where $T_{0\,m}$ is the percentage of time that the members of the dyad spent in body contact and $T_{2\,m}$ is the percentage of time they spent within 2 m of each other (see Huchard et al., 2010; Smuts, 1985).

To measure to what extent the focal female was attracted towards each male and assess her mate preferences, we used the approach index *Ia* during the mate-guarding period, calculated as *Ia = Na / (Na + Nd)*, where *Na* and *Nd* were the numbers of female approaches and departures involving a given male, respectively (see Hinde & Atkinson, 1970; Manson, 1992). We computed this index for female/male dyads for which 10 or more approaches and departures were recorded, that is, 95% of dyads (57/60).

We studied behavioural sequences in which the mate-guarding male responded to interaction between the oestrous female and a rival, that is, any male other than the mate-guarding individual. The first part of a behavioural sequence was an approach between the female and the rival male, performed by either partner. The next part of the sequence was the interaction which could occur between the female and the rival male. The last part was the response of the mate-guarding male. For two behaviours to be counted as part of the same sequence, they should occur within a 5-s interval.

2.5 | Statistical analyses

We performed general linear mixed model (GLMM) analyses using R 3.1.0 (R Core Team, 2015) and the LME4 package (Bates, Maechler, Bolker, & Walker, 2014). The individual identities of females (nested in the factor study site) and males (nested in the factor study site) as random factors were included in every model to control for pseudo-replication.

In a first analysis, we investigated behavioural sequences during the mate-guarding period to evaluate the consistency of direct and indirect choices made by females. We aimed to identify which interactions between the female and a male other than the mate-guarding individual induced a response from the latter, that is, approaching the female, mount, sexual interest, affiliation towards the female, affiliation towards the rival, interposition, aggression towards the female, aggression towards the rival. The target variable was the response of the mate-guarding male (response/no response). There were two predictor variables: the approaching individual (female/rival) and the interaction that may occur between the female and the rival (female affiliation towards the rival, female sexual presentation to the rival, rival affiliation towards the female, rival sexual interest, no interaction). We applied GLMM analyses using a binomial repartition and the logit link.

To investigate female mate preferences, we focused a second analysis on mating-related behaviours during mate-guarding and non-mate-guarding periods. Target variables were the number of sexual presentations by females and the number of mounts between males and females, both calculated over 3-hr periods. Predictor variables were the reproductive period (mate guarding/non-mate guarding) and the variables interacting with it, namely male partner category (guarding male/rival male), male dominance rank (top-ranking male/non-top-ranking male), proximity index, approach index and coefficient of maternal relatedness between female and male individuals. We also included female age and number of adult males as predictor variables due to their possible effect on sexual attractivity and/or levels of competition between males. As the frequencies of presentations and mounts corresponded to count data, we ran GLMM analyses using a Poisson distribution with a log link.

We first checked that there was no significant collinearity between predictor variables in all models (variance inflation factor lower than 3 for all variables). As several predictor variables could influence target variables, candidate sets of models were evaluated using an information-theoretic approach. After the selection of suitable predictors, we investigated the different possible combinations (Burnham & Anderson, 2002). Second-order Akaike information criterion (AICc) was used to determine the level of support for each model. Although the model with the lowest AICc value is often considered as the best-fitting model, any model within two AICc units of the lowest value is, by convention, considered to fit the data just as well (Burnham & Anderson, 2002). We therefore calculated the relative variable importance (RVI) for all predictor variables using the model.avg function of the MuMIn package (Barton, 2016). This allowed us to choose the best-fitting model by retaining the model that was within two AICc units of the lowest value, and which only contained variables with an RVI of at least 0.8 (Galipaud, Gillingham, David, & Dechaume-Moncharmont, 2014). We checked the normality of residuals in our best models by visualising Q–Q plots.

Once the best-fitting models had been identified using the AIC approach, we determined the significance of simple effects with the Wald test provided by LME4. We also performed post hoc analyses to better understand interaction results in GLMMs. For interactions between a quantitative and a qualitative variable, we ran post hoc analyses on the pairwise interaction contrasts using the testInteractions function from the PHIA package in R (De Rosario-Martinez, 2015). This method adjusts interaction *p*-values with a Holm–Bonferroni correction and removes the influences from the main effects in the model. For interactions between two qualitative variables, multiple pairwise comparisons with a Tukey's adjustment (Lenth, 2013) were run using least squares means via the LSMEANS package in R. Only the *p*-values of main effects that were not included in a statistically significant interaction were considered.

3 | RESULTS

3.1 | Descriptive data

The mate-guarding individual was the top-ranking male of the group for 11 of the 16 focal females: ten females were at least 7 years old, and one was 5 years old. The other five females were guarded by the male that was either second or third in rank in the male hierarchy: three of these females were 5 years old, whereas the other two were over 7 years old but were studied at a time when the top-ranking male was challenged by the second-ranking male of the group. Although most matings were performed by mate-guarding males, other males were responsible for 37 of 694 mounts during the guarding period. Twenty-one of these 37 mounts occurred on the first day of a guarding period when the mate-guarding individual was still frequently away from the female, and nine were surreptitious copulations occurring

TABLE 2 Results of Wald tests for the best-fitting general linear mixed model models retained using the Akaike information criterion (AICc) regarding the responses of the mate-guarding male to interactions between the oestrous female and male rivals

Target variables: responses of the mate-guarding male	Predictor variables: interactions between female and rivals	Estimate ± *SD*	*z*	*p*
Approach towards female (model 1: AICc = 785.1)	Approaching individual (rival vs. female)	−1.11 ± 0.22	−4.98	<.001
	Female sexual presentation (vs. no interaction)	−24 ± 9,099	<0.001	1
	Female affiliation (vs. no interaction)	0.341 ± 0.381	0.895	.371
	Rival affiliation (vs. no interaction)	−0.629 ± 0.750	−0.839	.401
	Rival sexual interest (vs. no interaction)	−20 ± 1,257	−0.002	.999
Affiliation towards rival (model 12: AICc = 215.7)	Approaching individual (rival vs. female)	2.64 ± 0.76	3.49	<.001
Interposition (model 14: AICc = 515.4)	Approaching individual (rival vs. female)	−1.08 ± 0.29	−3.65	<.001
Aggression towards female (model 16: AICc = 104.1)	Approaching individual (rival vs. female)	2.69 ± 1.14	2.37	.018
	Female sexual presentation (vs. no interaction)	2.90 ± 1.24	2.33	.020
	Female affiliation (vs. no interaction)	−19.2 ± 374	−0.051	.959
	Rival affiliation (vs. no interaction)	−25 ± 1,448	−0.017	.986
	Rival sexual interest (vs. no interaction)	3.17 ± 0.95	3.34	<.001

when the mate-guarding individual went inside the shelter to feed or drink for a few minutes. The seven remaining mounts were observed at a time when the second- and third-ranking males of the group formed a coalition and challenged the top-ranking male, allowing the second-ranking male to guard the oestrous female and mate with her (we recorded four instances where the female, Veo, responded with threat vocalisations to a solicitation by the top-ranking male, systematically inducing a conflict between the latter and the other males, who were supported by the female).

3.2 | Response of the mate-guarding male to interactions between the oestrous female and rival males during the mate-guarding period

The mate-guarding male showed different responses according to the type of approach and/or interaction occurring between the oestrous female and his rivals. The best-fitting model to explain the approach of the female by the mate-guarding male included both predictors: approaching individual and interaction between the female and a rival (Table S1: model 1). The mate-guarding male was more likely to approach the female when she was approaching a rival than when the latter was approaching her (Table 2). Social interactions between the female and a rival did not yield any significant effect although in the model (Table 2: female sexual presentation, female affiliation, rival affiliation, rival sexual interest).

The best-fitting models to explain affiliation, mount or sexual interest by the mate-guarding male did not include any predictor variables (Table S1: models 3, 7 and 10), so we did not investigate them further. For the other responses of the mate-guarding male, the best-fitting models only included the approaching individual (Table S1: affiliation towards rival, model 12; interposition, model 14). The mate-guarding male was more likely to address affiliative behaviours to a rival when the latter approached the female (Table 2: affiliation towards rival). The mate-guarding male was more likely to interpose himself between partners when the female approached the rival (Table 2: interposition).

The best-fitting model to explain male aggression towards the female partner included both predictor variables (approaching individual and interaction between female and rival, Table S1: model 16). The mate-guarding male was more likely to show aggression towards the female when a rival was approaching her, when she presented to the rival, or when the latter exhibited sexual interest (Table 2). The probability of male aggression towards the female was not significantly affected by displays of affiliative behaviour between the female and rival, regardless of which partner initiated them (Table 2).

Lastly, aggressive behaviours shown by the mate-guarding individual towards a rival always occurred when the female approached the rival and never when the latter approached the female, thus making statistical analysis unnecessary.

3.3 | Sexual partners of females during mate-guarding and non-mate-guarding periods

We found contrasting patterns of female partnership for sexual presentations and mounts during reproductive periods. The best-fitting model to explain sexual presentations (Table S2: model 1) contained the following independent predictors: reproductive period, male partner category, proximity index, approach index, number of males, and interactions between reproductive period and, respectively, male partner category, proximity index and approach index (Table 3). Presentations were less frequent in groups containing a larger number of males (Table 3). A post hoc analysis of the interaction between reproductive period and male partner category variables revealed that oestrous females presented more frequently to the guarding individual than to other males in both reproductive periods, and this effect was more pronounced during mate guarding (Figure 2a). Analysis of the interaction between reproductive period and proximity index

TABLE 3 Results of Wald tests for the best-fitting general linear mixed model models retained using the Akaike information criterion (AICc) regarding the frequencies of sexual presentations and mounts

	Presentations (model 1: AICc = 2,770.0)			Mounts (model 23: AICc = 1,953.0)		
Predictor variables	**Estimate ± *SD***	***z***	***p***	**Estimate ± *SD***	***z***	***p***
Reproductive period	1.73 ± 0.31	5.66	<.001	0.130 ± 0.438	0.296	.767
Male partner	3.30 ± 0.15	21.9	<.001	2.87 ± 0.21	13.4	<.001
Male dominance				−1.79 ± 0.70	−2.57	.010
Proximity index	0.809 ± 0.170	4.77	<.001	0.353 ± 0.197	1.79	.074
Approach index	1.82 ± 0.490	3.71	<.001	−0.937 ± 0.710	−1.32	.187
Relatedness				−1.14 ± 0.55	−2.08	.038
Number of males	−0.925 ± 0.236	−3.91	<.001			
Reproductive period × male partner	−2.13 ± 0.19	−11.4	<.001	−2.46 ± 0.29	−8.50	<.001
Reproductive period × male dominance				0.522 ± 0.226	2.31	.021
Reproductive period × proximity index	−1.24 ± 0.165	−7.48	<.001	−0.570 ± 0.248	−2.30	.022
Reproductive period × approach index	1.32 ± 0.49	2.67	.008	3.47 ± 0.80	4.31	<.001
Reproductive period × relatedness				−1.48 ± 0.70	−2.11	.035

variables indicated that females presented more frequently to males exhibiting a higher index than to other males with a lower index in the mate-guarding period, whereas the contrary was found during the non-mate-guarding period (Figure 2b). Analysis of the interaction between reproductive period and approach index variables showed that the higher the index of males, the more frequently females presented to them during both reproductive periods (Figure 2c).

The best-fitting model to explain mounts (Table S2: model 23) included the following predictors: reproductive period, male partner category, male dominance, proximity index, approach index, coefficient of relatedness, and interactions between reproductive period and, respectively, male partner category, male dominance, proximity index, approach index and coefficient of relatedness (Table 3). Analysis of the interaction between reproductive period and male partner variables revealed that females were mounted more often by the mate-guarding individual than by other males during mate guarding (Figure 2d). The interaction between reproductive period and male dominance variables indicated that top-ranking males mounted females more often during mate guarding; however, interaction analysis showed that differences between lower-ranking males and the top-ranking male remained non-significant throughout the non-mate-guarding period (Figure 2e). Analysis of the interaction between reproductive period and proximity index variables did not yield any significant independent effect in each reproductive period (Figure 2f). The interaction between reproductive period and approach index variables revealed that during mate guarding, females tended to be mounted less frequently by males with a higher index than by males with a lower index although the difference remained non-significant, while they were mounted significantly more frequently by males with a higher index during the non-mate-guarding period (Figure 2g). The interaction between reproductive period and relatedness variables showed that more closely related males mated with females less frequently than other males did during both reproductive periods (Figure 2h).

4 | DISCUSSION

In the studied population of Tonkean macaques, the males who successfully guarded parous females and mated with them were the highest-ranking males in almost all cases (11 of 12 females), as widely reported in non-human primates competing over mates (Cowlishaw & Dunbar, 1991; Muller & Wrangham, 2009). The four nulliparae were guarded by second- or third-rank individuals in the male social hierarchy. Young females in other primate species also appear to be less attractive to males than fully mature ones, which may be related to their lower fertility and high rates of reproductive failure (Gesquiere, Wango, Alberts, & Altmann, 2007; Setchell & Kappeler, 2003; Smuts, 1987). Another classic finding is the fact that matings were less frequent in Tonkean macaques when the sexual partners had higher levels of maternal relatedness. It is likely that the avoidance of genetic relatives works as a mechanism to prevent inbreeding (Manson, 2010; Soltis, 2004).

Analysis of the behavioural sequences occurring over the mate-guarding period showed that the guarding male actively reacted to the interactions occurring between the oestrous female and his rivals. His response often depended on which partner approached the other. The guarding male was more likely to move towards and/or threaten

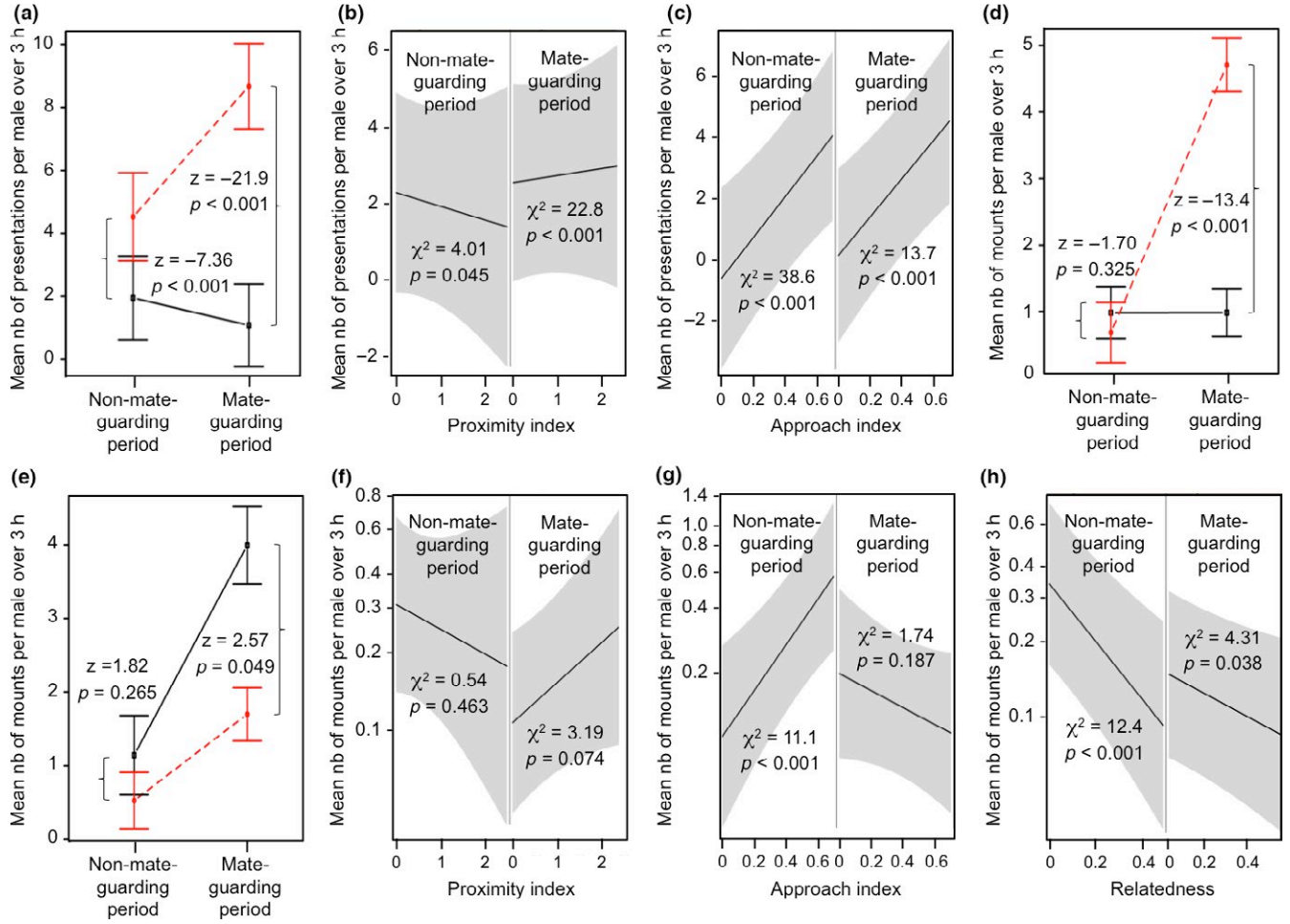

FIGURE 2 Statistical interactions in the analyses of sexual presentations and mounts: (a) presentations: reproductive period × male partner category, LSMeans post hoc comparison test (LSM phct), guarding males in red, rival males in black; (b) presentations: reproductive period × proximity index, interaction contrast with Holm–Bonferroni correction (ic HBc), *df* = 1; (c) presentations: reproductive period × approach index, ic HBc, *df* = 1; (d) mounts: reproductive period × male partner, LSM phct, guarding males in red, rival males in black; (e) mounts: reproductive period × male dominance, LSM phct, top-ranking males in black, low-ranking males in red; (f) mounts: reproductive period × proximity index, ic HBc, *df* = 1; (g) mounts: reproductive period × approach index, ic HBc, *df* = 1; (h) mounts: reproductive period × relatedness coefficient, ic HBc, *df* = 1. Error bars represent means and standards errors, and shading represents 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

the female when she approached another male than when she was approached, and when the female sexually interacted with males through sexual presentation, sexual solicitation and/or genital inspection. Through such herding behaviour (see Muller & Wrangham, 2009), the guarding individual aimed to constrain the female's behaviour and control his competitors, and it is noteworthy that he generally avoided threatening other males. He used aggression against the female when the latter approached other males, but generally did not do so when the female was approached by other males. In this case, the guarding individual was more likely to interpose himself between partners or display affiliative behaviours towards the rival; males do indeed monitor and reaffirm their social relationships through such greeting interactions (De Marco, Cozzolino, Dessì-Fulgheri, & Thierry, 2011b; De Marco et al., 2014). It should be added that females did not suffer any physical costs, nor did males used aggression to force reluctant females into copulation. We did not record any injuries to females or violent attacks on them, as reported in baboons (*Papio* spp.) and chimpanzees (*Pan troglodytes*; Muller & Wrangham, 2009; Smuts & Smuts, 1993). This shows that in a tolerant macaque species where the dominance gradient is typically low, mate-guarding individuals were able to coerce females, preventing them from mating with other males at conception time. Mate-guarding Tonkean macaques performed mild threats towards females at low frequencies (0.01 occurrence per hour), which was sufficient to dissuade them from continuing to interact with male rivals. Threats by males were actually more effective in Tonkean macaques than in intolerant species such as rhesus and Japanese macaques, where scramble competition usually drives females to respond to the aggression of high-ranking males by restoring proximity with their lower-ranking partner (Huffman, 1987; Manson, 1992, 2010). In sum, mate-guarding males successfully prevented fertile females from expressing direct mate choice in Tonkean macaques. This supports the view that indirect female choice plays a

predominant role in this species, while not necessarily acting in the same direction as direct female choice.

We examined direct female choice through the distribution of sexual presentations during oestrous periods. Males that maintained a stronger social bond with a female—as measured by the proximity index outside oestrous periods—received more presentations from her during mate-guarding periods compared to other males, but not during the non-mate-guarding period. Males that were more sought after by the female—as measured by the approach index during mate-guarding periods—received more presentations from the female in both reproductive periods compared to other males. In addition, the female presented to the mate-guarding individual more often than to the other males, not only throughout guarding but also during the non-mate-guarding period. The fact that females showed a greater attraction towards the males that had a stronger bond with her and those more sought after in the mate-guarding period does not support the graded-signal and the best-male hypotheses with respect to direct mate choice, as both predicted that fertile females should display an exclusive preference for dominant males. Quite to the contrary, females attempted to mate with other partners during mate guarding, a behaviour that is consistent with the weak-selectivity hypothesis. This result is in line with reports from other macaque species (Engelhardt et al., 2006; Manson, 2010; Nikitopoulos et al., 2005) and primates forming multimale–multifemale groups such as baboons (Clarke et al., 2009; Smuts, 1985) or grey-cheeked mangabeys (*Lophocebus albigena*; Arlet, Molleman, & Chapman, 2007).

Matings result from both direct and indirect mate choice. Moreover, the expression of female choice is often obscured by the operation of male competitive strategies (Nikitopoulos et al., 2005; Setchell & Kappeler, 2003; Small, 1989). Given that female Tonkean macaques had little direct control on partner selection during mate guarding, however, the distribution of their matings may be regarded primarily as an outcome of indirect mate choice, so it may be used in this context to assess the previous three hypotheses (best-male, graded-signal, weak-selectivity) with respect to indirect mate choice. Contrary to other males, guarding individuals mounted the oestrous female more often during the mate-guarding period, and dominant males were involved in most matings over the same period. Several males could openly mate with her until the first day of mate guarding, when the guarding male was not always present, but not later. The more sought-after males, for instance, exhibited higher mount frequencies during the non-mate-guarding period, that is, when the female was still free to move. To obtain sexual access to a female during the periovulatory phase, lower-ranking males had to make coalitions and separate the mate-guarding individual from the female or resort to surreptitious copulations when he was momentarily absent, but neither of these two tactics accounted for more than 1% of observed mounts. Furtive matings remain occasional in other primates too, and the incidence of challenging coalitions depends on species (Alberts, Buchan, & Altmann, 2006; Engelhardt et al., 2006; Soltis, 2004; Young, Hähndel, Majolo, Schülke, & Ostner, 2013). A main conclusion is that only males able to mate-guard had reproductive access to females at conception time in Tonkean macaques. This is consistent with the graded-signal and best-male hypotheses, but invalidates the weak-selectivity hypothesis regarding indirect mate choice.

The graded-signal hypothesis is based on the rationale that females should mate with multiple males in the period preceding the window of fertility to decrease the risk of males killing infants (Nunn, 1999; Zinner et al., 2004). However, infanticide by males is practically inexistent in macaque societies (van Schaik & Janson, 2000), and over 30 years of observation, we have not recorded any cases of infanticide by males in our study groups of Tonkean macaques, despite the regular occurrence of top-dominance takeovers between males. In these animals, like in several other species of primates, females promote indirect mate choice through sexual swellings which are honest signals of fertility (Aujard et al., 1998; Higham et al., 2012; Street et al., 2016; Thierry et al., 1996). Such swellings are voluminous ornaments that result from water retention induced by the rise in oestrogen levels, and this physiological process takes place over a long period of time (Dixson, 1983). Once maximal tumescence is achieved, it advertises to males that ovulation is approaching, setting the stage for heightened competition and the development of mate guarding, as proposed by the best-male hypothesis.[1] While the graded-signal hypothesis may also account for these phenomena, a more parsimonious explanation for the sexual interactions observed during the first period of oestrus is that females were not yet fully attractive to males, which is coupled with a very low probability of conception. Interestingly, another signal promoting indirect mate choice in Tonkean macaques is not dependent on morphological constraints, nor is it graded, namely the oestrous call, an unaddressed vocalisation that females emit at steady rates in the periovulatory phase and the 12 days preceding it (Aujard et al., 1998).

The current investigation concerned a captive population where males could not disperse into neighbouring groups. Further work is necessary to check whether the study of free-ranging Tonkean macaques would yield patterns similar to those brought to light by our analyses. An ongoing research programme will have also to verify that mate-guarding males are indeed the main genitors of their groups, as reported in other species (Engelhardt et al., 2006; Feldblum et al., 2014; Setchell & Kappeler, 2003). As a preliminary result, it may be worth mentioning that of the five females followed in the present study that gave birth to live born infants, all produced offspring that had been sired by the mate-guarding males (B. Thierry, H. Gachot, 2017). Recent studies in a wild group of crested macaques (*Macaca nigra*), another species from Sulawesi island, come to a similar conclusion: dominant males exerted mate guarding to coerce swollen females, and the top-ranking male fathered two-thirds of total offspring (Higham et al., 2012; Antje Engelhardt, personal communication).

[1]The reliable-indicator hypothesis proposes that females compete for the best males by honestly advertising their quality through costly genital swellings (Pagel, 1994). This hypothesis emphasizes between-female competition instead of between-male competition. However, no available evidence supports it (Nunn, 1999; Zinner et al., 2004), and a recent study in wild baboons (*Papio cynocephalus*) shows that males did not prefer females with larger swellings (Fitzpatrick, Altmann, & Alberts, 2015).

The strategies implemented by males depend on the balance of power between them (see (Kaburu & Newton-Fisher, 2015). It is important to bear in mind that the current study investigated the reproductive behaviours of males and females mainly during times of social stability. In one instance, the top-ranking male was challenged by two lower-ranking males who had allied against him. Throughout the years, however, we witnessed several periods of social instability when coalitions hindered the capacity of the top-ranking male to claim exclusive access to oestrous females; it remains to be seen whether the latter are more able to express direct mate choice during such periods. Furthermore, males are commonly considered to manipulate the opposite sex through sexual coercion. This seems true at the individual level, where they impose their will on females (Muller & Wrangham, 2009; Smuts & Smuts, 1993). Nonetheless, from an evolutionary point of view, females exerted indirect mate choice by promoting male–male competition, which in return reduced their ability to express direct mate choice. An intriguing question for the future is to understand which factors lead females to favour one strategy to another when choosing their mates (see Hosken, Alonzo, & Wedell, 2016; Wiley & Poston, 1996).

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REFERENCES

Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From mating opportunities to paternity success. *Animal Behaviour*, *72*, 1177–1196.

Altmann, S. A. (1962). A field study of the sociobiology of rhesus monkeys (*Macaca mulatta*). *Annals of the New York Academy of Sciences*, *102*, 338–435.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227–265.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Arlet, M. Z., Molleman, F., & Chapman, C. (2007). Indications for female mate choice in grey-cheeked mangabeys *Lophocebus albigena johnstoni* in Kibale National Park, Uganda. *Acta Ethologica*, *10*, 89–95.

Aujard, F., Heistermann, M., Thierry, B., & Hodges, J. K. (1998). Functional significance of behavioral, morphological, and endocrine correlates across the ovarian cycle in semifree ranging female Tonkean macaques. *American Journal of Primatology*, *46*, 285–309.

Barton, K. (2016). *MuMIn: multi-model inference. R package version 1.15.6*. Retrieved from https://cran.r-project.org/web/packages/MuMIn/

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version*, 1(7). Retrieved from https://cran.r-project.org/web/packages/lme4

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.

Clarke, P. M. R., Henzi, S. P., & Barrett, L. (2009). Sexual conflict in chacma baboons, *Papio hamadryas ursinus*: Absent males select for proactive females. *Animal Behaviour*, *77*, 1217–1225.

Clutton-Brock, T. (2009). Sexual selection in females. *Animal Behaviour*, *77*, 3–11.

Clutton-Brock, T. H., & Harvey, P. H. (1976). Evolutionary rules and primate societies. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 195–237). Cambridge: Cambridge University Press.

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, *20*, 37–46.

Cowlishaw, G., & Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, *41*, 1045–1056.

Cox, C. R., & Le Boeuf, B. J. (1977). Female incitation of male competition: A mechanism in sexual selection. *The American Naturalist*, *111*, 317–335.

De Marco, A., Cozzolino, R., Dessì-Fulgheri, F., & Thierry, B. (2011a). Collective arousal when reuniting after temporary separation in Tonkean macaques. *American Journal of Physical Anthropology*, *146*, 457–464.

De Marco, A., Cozzolino, R., Dessì-Fulgheri, F., & Thierry, B. (2011b). Interactions between third parties and consortship partners in Tonkean macaques (*Macaca tonkeana*). *International Journal of Primatology*, *32*, 708–720.

De Marco, A., Sanna, A., Cozzolino, R., & Thierry, B. (2014). The function of greetings in male Tonkean macaques. *American Journal of Primatology*, *76*, 989–998.

de Ruiter, J. R., van Hooff, J. A. R. A. M., & Scheffrahn, W. (1994). Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour*, *129*, 203–224.

Demaria, C., & Thierry, B. (2001). A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour*, *138*, 397–410.

Dixson, A. F. (1983). Observations on the evolution and behavioral significance of 'sexual skin' in female primate. *Advances in the Study of Behavior*, *13*, 63–106.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*, 215–223.

Engelhardt, A., Heistermann, M., Hodges, J. K., Nürnberg, P., & Niemitz, C. (2006). Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*)—male monopolisation, female mate choice or post-copulatory mechanisms? *Behavioral Ecology and Sociobiology*, *59*, 740–752.

Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Paiva, T., Mine Cetinkaya-Rundel, M., … Gilby, I. C. (2014). Sexually coercive male chimpanzees sire more offspring. *Current Biology*, *24*, 2855–2860.

Fitzpatrick, C. L., Altmann, J., & Alberts, S. C. (2015). Exaggerated sexual swellings and male mate choice in primates: Testing the reliable indicator hypothesis in the Amboseli baboons. *Animal Behaviour*, *104*, 175–185.

Galipaud, M., Gillingham, M. A. F., David, M., & Dechaume-Moncharmont, F. X. (2014). Ecologists overestimate the importance of predictor variables in model averaging: A plea for cautious interpretations. *Methods in Ecology and Evolution*, *5*, 983–991.

Georgiev, A. V., Muehlenbein, M. P., Prall, S. P., Emery Thompson, M., & Maestripieri, D. (2015). Male quality, dominance rank, and mating success in free-ranging rhesus macaques. *Behavioral Ecology*, *26*, 763–772.

Gesquiere, L. R., Wango, E. O., Alberts, S. C., & Altmann, J. (2007). Mechanisms of sexual selection: Sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. *Hormones and Behavior*, *51*, 114–125.

Herrenschmidt, N. (1977). Semi-free breeding of tropical Celebes macaques (*Macaca tonkeana*) in a continental European climate. *Journal of Medical Primatology*, *6*, 58–65.

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, *12*, 89.

Hinde, R. A., & Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother–infant relations in rhesus monkeys. *Animal Behaviour*, *18*, 169–176.

Hosken, D. J., Alonzo, S. H., & Wedell, N. (2016). Why aren't signals of female quality more common? *Animal Behaviour*, *114*, 199–201.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13–40.

Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2010). More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behavioral Ecology and Sociobiology*, *64*, 769–781.

Huffman, M. A. (1987). Consort intrusion and female mate choice in Japanese macaques (*Macaca fuscata*). *Ethology*, *75*, 221–234.

Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male–male competition, female mate choice and their interaction: Determining total sexual selection. *Journal of Evolutionary Biology*, *22*, 13–26.

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, *69*, 1039–1052.

Kappeler, P. M., & van Schaik, C. P. (2004). *Sexual selection in primates: New and comparative perspectives*. Cambridge: Cambridge University Press.

Lenth, R. V. (2013). *Lsmeans: least-squares means. R package version 1.06-05*. Retrieved from http.CRAN.R-project.org/package=lsmeans

Manson, J. H. (1992). Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, *44*, 405–416.

Manson, J. H. (2010). Mate choice. In C. Campbell, A. Fuentes, K. MacKinnon, S. Bearder, & R. Stumpf (Eds.), *Primates in perspective* (pp. 476–488). Oxford: Oxford University Press.

Muller, M. N., & Wrangham, R. W. (2009). *Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press.

Nikitopoulos, E., Heistermann, M., de Vries, A., van Hooff, J. A. R. A. M., & Sterck, E. H. M. (2005). A pair choice test to identify female mating pattern relative to ovulation in longtailed macaques, *Macaca fascicularis*. *Animal Behaviour*, *70*, 1283–1296.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, *58*, 229–246.

O'Connell, S. M., & Cowlishaw, G. (1994). Infanticide avoidance, sperm competition and mate choice: The function of copulation calls in female baboons. *Animal Behaviour*, *48*, 687–694.

Pagel, M. (1994). The evolution of conspicuous oestrous advertisement in Old World monkeys. *Animal Behaviour*, *47*, 1333–1341.

Paul, A. (2004). Dominance and paternity. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 131–134). Cambridge: Cambridge University Press.

Petit, O., & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour*, *48*, 1427–1436.

R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

De Rosario-Martinez, H. (2015). *Phia: post-hoc interaction analysis. R package version 0.2-1*. Retrieved from https://cran.r-project.org/package=phia

Sanna, A., De Marco, A., Thierry, B., & Cozzolino, R. (2015). Growth rates in a captive population of Tonkean macaques. *Primates*, *56*, 227–233.

Setchell, J. M., & Kappeler, P. M. (2003). Selection in relation to sex in primates. *Advances in the Study of Behavior*, *33*, 87–171.

Small, M. F. (1989). Female choice in nonhuman primates. *Yearbook of Physical Anthropology*, *32*, 103–127.

Smuts, B. B. (1985). *Sex and friendship in baboons*. New York, NY: Aldine.

Smuts, B. B. (1987). Sexual competition and mate choice. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 385–399). Chicago, IL: University of Chicago Press.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior*, *22*, 1–63.

Soltis, J. (2004). Mating systems. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 135–151). Cambridge: Cambridge University Press.

Street, S. E., Cross, C. P., & Brown, G. R. (2016). Exaggerated sexual swellings in female nonhuman primates are reliable signals of female fertility and body condition. *Animal Behaviour*, *112*, 203–212.

Stumpf, R. M., Martinez-Mota, R., Milich, K. M., Righini, N., & Shattuck, M. R. (2011). Sexual conflict in primates. *Evolutionary Anthropology*, *20*, 62–75.

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology*, *16*, 224–238.

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C., & Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In J. J. Roeder, B. Thierry, J. R. Anderson, & N. Herrenschmidt (Eds.), *Current primatology, Vol. 2: Social development, learning and behaviour* (pp. 103–117). Strasbourg: Université Louis Pasteur.

Thierry, B., Heistermann, M., Aujard, F., & Hodges, J. K. (1996). Long-term data on basic reproductive parameters and evaluation of endocrine, morphological, and behavioral measures for monitoring reproductive status in a group of semifree-ranging Tonkean macaques (*Macaca tonkeana*). *American Journal of Primatology*, *39*, 47–62.

Tiddi, B., Wheeler, B. C., & Heistermann, M. (2015). Female behavioral proceptivity functions as a probabilistic signal of fertility, not female quality, in a New World primate. *Hormones and Behavior*, *73*, 148–155.

van Noordwijk, M. A., & van Schaik, C. P. (2000). Reproductive patterns in eutherian mammals: Adaptations against infanticide? In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 322–360). Cambridge: Cambridge University Press.

van Schaik, C. P., & Janson, C. H. (2000). *Infanticide by males and its implications*. Cambridge: Cambridge University Press.

van Schaik, C. P., Pradhan, G. R., & van Noordwijk, M. A. (2004). Mating conflict in primates: Infanticide, sexual harassment and female sexuality. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 131–150). Cambridge: Cambridge University Press.

Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765–778.

Wiley, R. H., & Poston, J. (1996). Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, *50*, 1371–1381.

Wong, B. B. M., & Candolin, U. (2005). How is female mate choice affected by male competition? *Biological Reviews*, *80*, 559–571.

Young, C., Hähndel, S., Majolo, B., Schülke, O., & Ostner, J. (2013). Male coalitions and female behaviour affect male mating success independent of dominance rank and female receptive synchrony in wild Barbary macaques. *Behavioral Ecology and Sociobiology*, *67*, 1665–1677.

Zinner, D. P., van Schaik, C. P., Nunn, C. L., & Kappeler, P. (2004). Sexual selection and exaggerated sexual swellings of female primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 71–85). Cambridge: Cambridge University Press.

SUPPORTING INFORMATION

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RESEARCH ARTICLE

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Effect of reward type on object discrimination learning in socially monogamous coppery titi monkeys (*Callicebus cupreus*)

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Highly valued food items are often used as rewards to reinforce an animal's behavior. For social species, social interaction is rewarding and can drive an individual's behavior as well. In the currently study, we wanted to compare the efficacy of a food reward and a social reward on object discrimination learning in socially monogamous titi monkeys. We hypothesized that titi monkeys would perform more accurately for a social reward (their pair mate) than for a food reward (a highly desired food item). Eleven adult titi monkeys were tested with a two-object visual discrimination task for both types of reward. The colors and shapes of the objects in the two-object discrimination task were counterbalanced across subjects. During each trial, subjects were shown two objects, and the trial ended when the subject touched the reinforced shape (S+) or after 5 min. A correct trial was defined as one when the subject touched S+ first. We found that 45.5% of subjects were able to learn the task with a social reward, and 83.3% were able to learn the task with a food reward. We found that subjects balked more often and had fewer correct trials for the social reward. Finally, subjects took longer to approach the shapes for a social reward, possibly indicating lower motivation to engage in the task when a social reward is used compared to a food reward. Although significantly fewer subjects met criteria of success with the social reward than with the food reward, our results show that titi monkeys can learn a visual discrimination task with either type of reward.

KEYWORDS
monogamy, nonhuman primate, positive reinforcement, social reward, visual discrimination

1 | INTRODUCTION

Operant, or instrumental, conditioning is a type of animal learning where the strength or frequency of a certain behavior is altered by positive reinforcement (reward) or negative reinforcement (punishment). In operant conditioning, also referred to as associative learning, an animal also learns to associate certain signals with the positive or negative consequences of their behavior. Operant conditioning has been studied for over a century (Skinner, 2012; Thorndike, 1898), and numerous studies have now contributed to a rich understanding of the environmental and biological factors that underlie animal learning across many species, including invertebrates (Hawkins & Byrne, 2015), birds (Park, Okanoya, & Dooling, 1985), fish (Lucon-Xiccato & Bisazza, 2016; Thompson & Sturm, 1965), and mammals (Grant, 1964), including monkeys (Alvarado, Malkova, & Bachevalier, 2016).

Many behavioral tests that were designed to assess animal learning rely on an animal's ability to discriminate between two stimuli,

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such as sounds or objects, which are paired with reinforcing or neutral outcomes. The simplest version of this concept is classical conditioning, in which a single, neutral stimulus, such as a bell (conditioned stimulus), gains the ability to trigger a conditioned response after repeated pairings with the unconditioned stimulus, such as a food reward (Pavlov, 1960). It is possible to expand the number of stimuli to include two objects or sounds, and only pair one of them with a reinforcer, in order to test a subject's ability to distinguish between the two and selectively respond to the conditioned stimulus.

This approach is referred to discrimination learning, and much of the early work to understand this type of learning in nonhuman primates was done by Harlow and colleagues (Harlow, 1945; Moss & Harlow, 1947), who also developed the Wisconsin General Test Apparatus (WGTA) to test the learning abilities of rhesus macaques (Harlow & Bromer, 1938). One way that the WGTA can be used is in a two-object visual discrimination task, in which two objects that differ in shape, size, and/or color are presented side-by-side to a test subject. For positive reinforcement learning, after repeated trials in which one of the objects is paired with a reward, a subject will learn the difference between the stimuli and will consistently respond only to the stimulus that is associated with a reward. The studies employing the WGTA have provided a framework upon which our understanding of nonhuman primate learning have been built, including marmosets (Ridley, Bowes, Baker, & Crow, 1984), capuchins (Tavares & Tomaz, 2002), and baboons (Deruelle, Barbet, Dépy, & Fagot, 2000), and it has also been modified for use in rats (Rollin, Thaller, & Shepp, 1963).

Frequently, in studies of animal learning, food is used as the rewarding stimulus for positive reinforcement. Comparatively, relatively few studies of animal learning have used social rewards, such as gaining access to one or more conspecifics, to assess the animal learning. However, a variety of studies have provided evidence that different categories of social interactions are rewarding for animals (Trezza, Campolongo, & Vanderschuren, 2011). For example, it has been demonstrated in mice that social play among juveniles is rewarding (Panksepp & Lahvis, 2007). In addition, mother rats will learn complex mazes to be with their litters, and they will perform more crossings of an electrified grid in order to gain access to their litters than they would to gain access to water or food after water or food deprivation (Wilsoncroft, 1968). In addition, early postpartum, lactating dams find interactions with pups more rewarding than cocaine (Mattson, Williams, Rosenblatt, & Morrell, 2003, 2001), even when the dose of cocaine is increased (Seip & Morrell, 2007). Thus, a social reward, in this case the offspring, can act as an efficient motivator and a reinforcer for performance on a task. Rats will also work to free a trapped, familiar cage mate from a restraining enclosure, even if they are presented with a concurrent, alternative choice to open a container containing chocolate chips (Bartal, Decety, & Mason, 2011). In socially monogamous prairie voles, cohabitation with mating, which begins the process of pair-bond formation, produces a conditioned place preference in males, which indicates that this interaction is rewarding (Ulloa et al., 2017). Nonhuman primates have also been shown to find social stimuli rewarding, and gaining visual access to a conspecific or a photograph or video of a conspecific have been successfully used as reinforcers in studies of primate learning (Anderson, 1998; Butler, 1954; Deaner, Khera, & Platt, 2005; Gray, Pearce, Thiele, & Rowe, 2017).

If social rewards can reinforce an individual's learning, then this effect should be particularly strong in species that form strong social bonds, such as monogamous species, in which adult male-female pairs form a lasting attachment relationship after mating. Thus, we hypothesized that for a pair-bonded individual of a monogamous species, that individual's pair mate should act as an efficient positive reinforcer in learning tasks. The current study used coppery titi monkeys (*Callicebus cupreus)*, which are monogamous, New World primates (Bales et al., 2017). Adults in this species form a stable, bidirectional social bond between opposite sexed individuals after mating (Mason, 1974). Once bonded, titi monkeys prefer to spend extended periods of time in close physical proximity to their pair mate (Anzenberger, 1988; Mendoza & Mason, 1997). Previous studies in titi monkeys have used the WGTA to assess their ability to learn to associate an object with a food reward outcome (Fragaszy, 1981), but it has not been determined whether a social reward would also act as a potent reinforcer in an object discrimination learning task for this species. Based on their ability to learn cognitive tasks and their strong monogamous attachments, titi monkeys are an excellent animal model for the study of social reward efficiency.

In the current study, we developed a two-object visual discrimination task that was modeled roughly after the features of the WGTA and was adapted for testing titi monkeys in their home cage environment. The two reinforcing stimuli for the task were either gaining access to a highly desired food item (food reward) or gaining access to their pair mate (social reward). We sought to determine if the subject's pair mate would serve as an effective positive reinforcer in the discrimination task. We also wanted to directly compare the efficacy of a food reward and a social reward on titi monkey learning outcomes. Compared to the food reward, we predicted that individuals who were being tested with the social reward should (a) need fewer trials to reach the criterion for successfully learning to discriminate two objects, (b) balk less, and (c) make fewer incorrect choices. This study expands previous investigations of learning in titi monkeys and expands our knowledge of the value of social bonding in this species.

2 | MATERIALS AND METHODS

2.1 | Animals

Subjects were 28 adult laboratory-born titi monkeys who had been living as heterosexual pairs in stable family units at the California National Primate Research Center in Davis, CA. All testing took place between November 2013 and January 2014. Their age ranged from 2.2 to 24.0 years old (mean ± SD = 7.9 ± 5.5 years). Animals were housed in living cages (1.2 × 1.2 × 2.1 m) that were situated such that each family group was visually isolated from others, but auditory and olfactory interactions were possible. All cages were equipped with four perches. Animals were on a 12:12 light: dark cycle with lights on at 0600 and lights off at 1800. Temperature was maintained at 21 °C.

Animals were fed a diet of monkey chow, rice cereal, apple, and carrot at 0800 and at 1300. Water was available ad libitum. Subjects were living with their pair mate only or with their pair mate and offspring. None of the subjects had ever participated in a discrimination-learning experiment before. This research complied with protocols that were reviewed and approved by the Institutional Animal Care and Use Committee of the University of California Davis, adhered to the legal requirements of the United States of America, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

2.2 | Test apparatus

In order to minimize negative effects of novel surroundings (Cubicciotti & Mason, 1975; Mendoza & Mason, 1986), all testing was carried out in the animal's home cage (Figure 1). During testing, a pair of shapes was fastened to the outside the cage, in front of a perch and in reach of the subject. The "trial zone" was defined as the ~14 cm^3 zone immediately surrounding this perch, where titi monkeys regularly sit in order to interact with lab members or care providers. The visual discrimination task used wooden shapes: triangles, squares, and circles (base × height = 11 × 11 cm, side × side = 12 × 12 cm, radius = 6.5 cm). Each shape was painted with acrylic paint (Craft smart®, water based) and covered with semigloss polyurethane sealant (Varathane®, water based) for easy cleaning. All males and half of the females of this species are dichromatic, so we painted the shapes black, white, and gray rather than using color (Bunce et al., 2011).

2.3 | Training

Before testing, subjects went through a training period in order to shape their behavior and habituate them to both the testing procedure and the brief separation from their pair mate (and offspring, if relevant). This training also helped to avoid any issues related to object novelty, which could be an issue with this highly neophobic species (Mayeaux & Mason, 1998). Due to the prevalence of neophobia in this species, we expected a considerable portion of subjects to fail this training phase, simply because of their unwillingness to approach novel objects. This training phase also served the purpose of determining which individuals exhibited enough novelty seeking behavior to be ideal subjects for further testing.

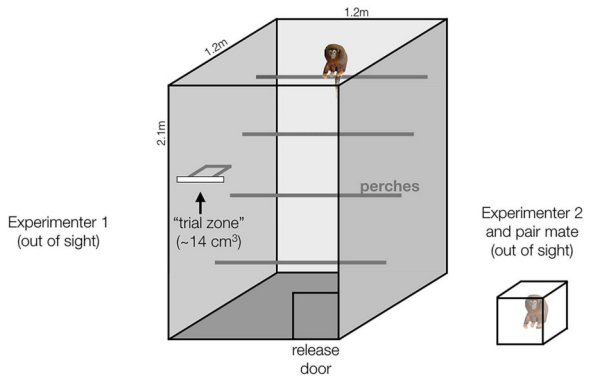

FIGURE 1 Schematic of the testing set-up in the subject's home cage

Before training began, the subject's pair mate and any offspring were caught and removed from the home cage for the duration of the training session (one male subject was occasionally carrying his infant offspring). The transport cage containing the subject's pair mate (and offspring, if applicable) was moved to a distant part of the room, out of visual range but still within auditory range of the subject; the transport box was covered with a towel, to calm the pair mate and reduce the likelihood of vocalization. Subjects were first trained to approach the trial zone and sit on the perch to get a peanut as a reward. Then, subjects were trained to reach out and touch any shape that was presented in the front of their cage. The shapes that were used in the training phase included any of the nine options that were used for testing (white, gray, or black circles, triangles, or squares) and were chosen at random throughout training so that the subjects would not habituate to or form preferences for any specific shape/color. The training was composed of 3–6 trials per day, with each training trial lasting at most 2 min. The training lasted until the monkey reached the criterion of stability: the subject approaches and grabs the shape without any peanut cue for 5 successive days. Time of training alternated between mornings (10:30–12:30) and afternoon (1:30–4:30). From the 28 animals that began training, 12 animals (7 males, 5 females) met criteria to continue to the testing phase of the experiment. The age of these 12 animals ranged from 2.2 to 24.0 years old (mean ± SD = 7.9 ± 5.5 years). The length that each animal had been paired with their pair mate ranged from 2 months to 5.9 years and was taken into account in the analysis (mean ± SD = 21.1 ± 24.7 months).

2.4 | Two-object discrimination task

After successfully meeting success criteria for training, animals were assigned to one of two groups based on the type of reinforcer that would be used for their first round of discrimination testing: food reward first or social reward first. The purpose of this task was to test whether animals can learn to distinguish two different shapes of different colors. For all tests, the subject's pair mate (and offspring, if applicable) were removed from the home cage as described above, and placed out of view of the test subject but within reach of one experimenter. Subjects were shown a pair of two different shapes of different colors, which were quickly clamped in place in the front of their cage so that a second experimenter could step out of view immediately after the start of a trial. One shape was predesignated as the "correct" or reinforced shape (S+) and the other as the non-reinforced shape (S−). Colors, shapes, and assignment as S+ or S− were counterbalanced across individuals. A correct response was defined as touching S+, and an incorrect response was defined as touching S−. If a correct response was given, the subject received the reinforcer immediately. In the food condition, a piece of a high value food (banana) was presented to the test subject in the palm of the experimenter who was located out of view of the monkey, but close

enough to the trial zone to present the food reward within reach of the test subject. After a correct response in the social condition, the test subject's pair mate was released into the home cage from the release door (Figure 1), a process that was initiated immediately by the experimenter who had been standing within reach of the transport cage but out of view of the test subject. After a correct response was given, the trial was over.

If an incorrect response was given (touching S−), nothing happened, and the subject could try again until a correct response was given or until the end of 5 min. The shapes were not repositioned if an incorrect response was made; the shapes remained in place until the subject touched S+ or until the end of 5 min. Balks were defined as trials in which no response was made before the end of 5 min. Incorrect trials were defined as trials in which only an incorrect response was made and no correct response was made before the end of 5 min. Presentation sides (left vs. right) of S+ were counterbalanced across trials. Subjects received two trials per day. After the shapes were presented, the latency to enter the trial zone and the latency to touch both S+ and S− were also measured.

When a trial was over, the stimulus shapes were removed from the front of the cage, and the pair mate was returned after at least a 2-min delay, in order to prevent the pair mate's return from being contingent on the subject's behavior during testing. Thus, there was no punishment for not performing the correct behavior. After a subject performed 10 correct trials in 12 successive sessions, the subject was considered to have reached criteria as successfully learning to choose S+. After this criterion was met, the animal began testing on the other type of reinforcer. In round 2 of testing, a different shape of a different color from the two that were previously used in round 1 was designated as the new reinforced shape (S+') for the second reinforcer. The S− remained the same. All individuals completed testing for both types of reward. If an animal balked in five out of six successive trials, their testing for that reinforcer was ended, and they were considered to have failed to meet criteria for successful learning of the discrimination task. Individuals with more than 30 trials without meeting the success criterion were also considered to have failed to meet criteria for successful learning of the discrimination task.

2.5 | Analysis

Data was analyzed using a general linear mixed model to determine the effects of the following variables on our outcome measures (described in Table 1): reward type (food vs. social), the order of testing (food first vs. social first), the length of the pair bond (number of days since pairing), sex, and age, as well as potential interactions. Animal ID was included as a random factor in order to account for individual differences. Twelve subjects were tested, but we dropped one subject because she balked in five out six trials in a row, so all analyses were done on the remaining 11 subjects. Residuals for all tests were normally distributed. p values of less than 0.05 were considered statistically significant.

TABLE 1 Outcome measures

Average latency (sec) to enter the trial zone
Average latency (sec) to make a correct choice after entering the trial zone
Average latency (sec) to make an incorrect choice after entering the trial zone
Percent of correct trials
Percent of trials where no correct response was given
The percent of trials where the subject balked
The number of trials to reach criteria

3 | RESULTS

The aim of the current study was to compare the effectiveness of the food and the social reward on monkeys' performance in a two-object visual discrimination task. There were no significant effects of the testing order on any of the outcome measures listed in Table 1, so we eliminated order as a variable and collapsed the data for further analyses. We found no significant sex differences, and there were no effects of pair bond length on any of our outcomes in the social reward condition.

We found a significant effect of reward type on the latency to enter the trial zone ($F[1,21] = 7.84$; $p = 0.023$; $eta^2 = 0.398$), such that the animals had a shorter latency to engage in the task when they were tested with a food reward than when they are tested with a social reward (Figure 2). However, there was no effect of reward type on the latency to make either a correct or incorrect response once the subject had entered the trial zone (Figure 2). In other words, once the subjects decided to enter the trial zone, they did not take additional time to decide which shape to choose.

We found several significant effects of the type of reward on performance and accuracy. First, we found a significant effect of reward on the percentage of correct trials ($F[1,21] = 8.41$; $p = 0.020$; $eta^2 = 0.292$) such that animals tested with a food reward had more correct trials than when they were tested with a social reward (Figure 3a). We found a significant effect of the reward on the number

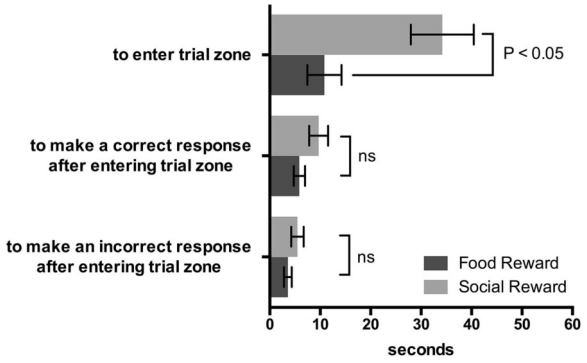

FIGURE 2 Average behavioral latencies during the two-object discrimination task between the two types of reward

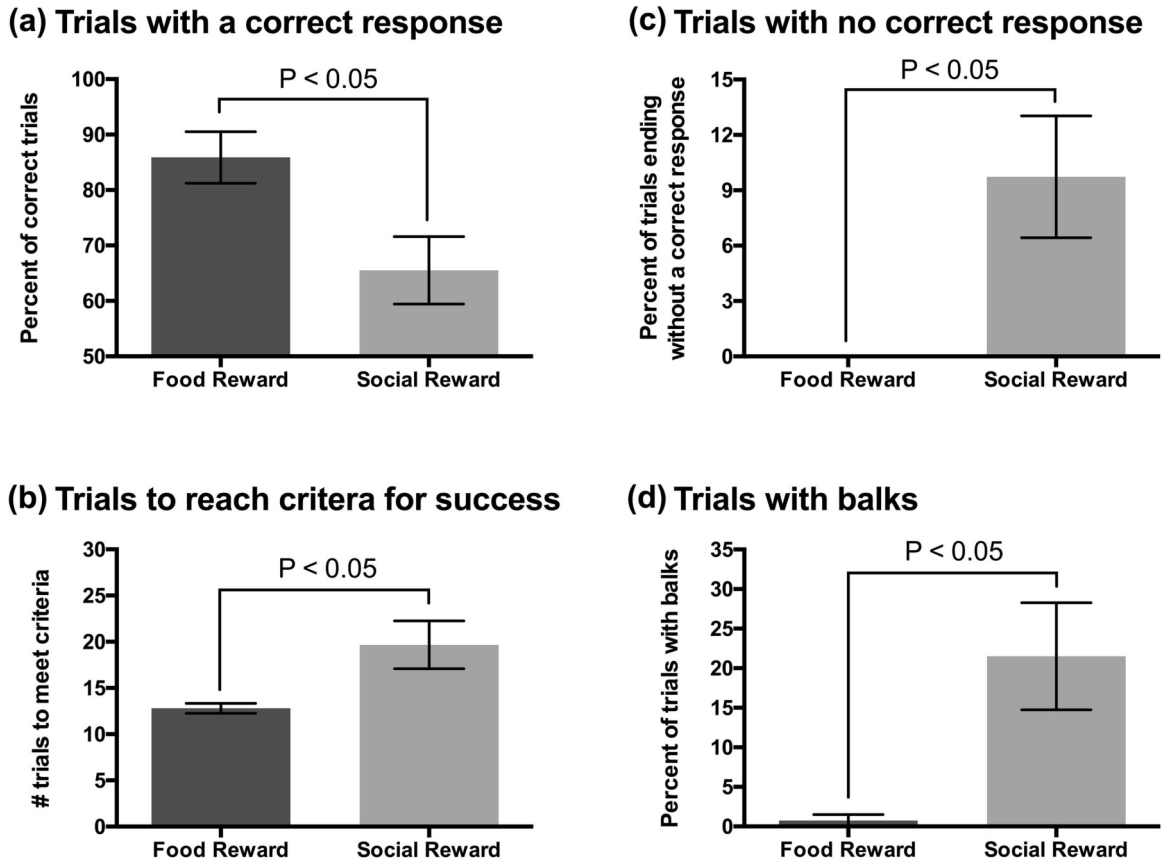

FIGURE 3 Learning outcomes in a two-object visual discrimination task. (a) Percent of trials ending with a correct response. (b) Number of trials required to reach success criteria. (c) Percent of trials ending with an incorrect response only and no correct response ever given. (d) Percent of trials when the subject balked

of trials needed to reach the criterion of success ($F[1,21] = 5.77$; $p = 0.043$; $eta^2 = 0.223$); animals working for a food reward succeeded after fewer trials than when they were working for a social reward (Figure 3b). We found the social group had a significantly higher percent of trials that ended with an incorrect response only ($F[1,21] = 6.48$; $p = 0.034$; $eta^2 = 0.401$). Only subjects of the social group had trials that ended with choosing S−; every subject in every trial with the food reward eventually touched S+ (Figure 3c). Finally, there was a significant effect of the type of reward on the percent of trials where the animal balked ($F[1,21] = 9.14$; $p = 0.017$; $eta^2 = 0.457$); the social group had a significantly higher percentage of trials with balks than the food group (Figure 3d). Although a higher proportion of animals succeeded in learning a two-object visual discrimination task when tested for a food reward compared to a social reward (Figure 4), nearly half of the animals tested with a social reward (45.5%) succeeded in learning the task.

4 | DISCUSSION

This study is the second to our knowledge to assess learning capacities in the coppery titi monkey. In the previous study, it was found that titi monkeys can learn to associate an object with a food reward (Fragaszy, 1981). Our current study extended these previous findings by examining whether a social reward can act as a reinforcer for this species and by directly comparing food reward and social reward in the same task. Our results confirmed previous findings that titi monkeys are capable of learning by positive reinforcement. Our findings also indicated that they could be trained to distinguish two objects with either a food reward or a social reward. However, it is important to note that these two reward types were examined only in this one

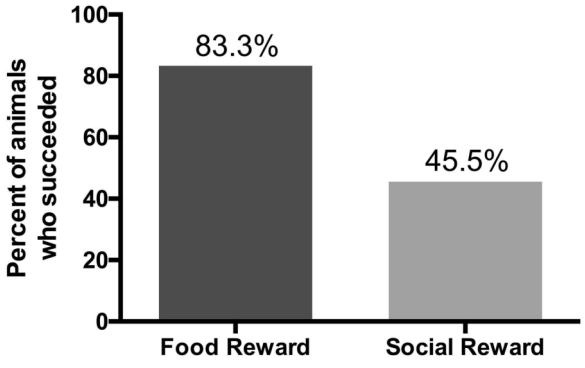

FIGURE 4 Percent of animals who succeeded in learning the two-object discrimination task

experimental situation—a visual object discrimination task—so future studies are warranted to evaluate their relative effectiveness across a wider range of testing conditions.

However, we found that a social reward is a less effective reinforcer of titi monkey learning in a discrimination task than a food reward. Our results supported this idea in several ways. When a social reward was used, titi monkeys had a higher proportion of incorrect trials, had trials when no correct response is ever given, and balked more often. For the 45.5% of animals who successfully learned the discrimination task with a social reward, they required more trials in order to reach criteria of success than the animals tested with a food reward.

In addition, we found that monkeys who are tested with the social reward take longer to enter the trial zone than monkeys who are tested with a food reward. This result could be interpreted in two different ways. The subjects could have been less motivated to participate in the two-object discrimination task when they are working for the return of their pair mate compared to a food reward. Alternatively, they may have taken longer to decide which was the correct shape, and this decision making process was occurring before they entered the trial zone. Our results indicated that the subjects did not take additional time to decide which shape to choose once they arrived in the trial zone; they made a choice as soon as they landed in the trial zone, and there were no differences in the latency to choose the correct or incorrect shape. Thus, it is possible that the subjects were deciding what shape to choose during the latency period between the time the shapes were presented and when they jumped to the perch in the trial zone. If this was the case, then animals tested for the social reward were taking more time to make the decision of which shape is S+, which would support the rest of our findings that social reward was a less effective reinforcer of their behavior.

Taken together, these results indicate that food was a more effective reinforcer of titi monkey behavior than a social reward, which is not what we hypothesized for this highly social, monogamous species. Titi monkeys form lasting pair bonds with their mate and show behavioral and endocrine markers of stress (agitation and increased plasma cortisol) when they are involuntarily separated from their pair mate (Fernandez-Duque, Mason, & Mendoza, 1997; Mendoza & Mason, 1986). Thus, we hypothesized that the return of their pair mate (a rewarding social stimulus) would be a potent reinforcer of their behavior and would be more efficient than a food reward. However, our results did not support this idea. It is possible that the subjects were experiencing some mild separation stress during our testing sessions (because the pair mate was removed prior to all tests), which could have impacted their behavior during testing. However, because the removal of the pair mate was consistent across both the food and social reward conditions, it is unlikely that stress from social separation impacted their behavior only in the social reward tests. In fact, if there were a differential effect of social separation on their behavior in these tests, we would assume that it would act as a motivator specifically in the social reward condition to increase their effort to end the separation by choosing S+, but this was not the case. Furthermore, the pair mate was removed during all training sessions prior to the testing phase of the experiment, which should minimize any effect of social separation on cognitive outcomes. We also did not note any behavioral signs of distress/arousal, such as distress calling, self scratching, or pacing, during any of our testing sessions. Thus, the increased latency to enter the trial zone and decreased accuracy of responses indicates to us that the pair mate's return was a less effective reinforcer than food in this monogamous species.

There are some potential caveats in our test design that are worth discussing in the context of our results. First, the stimulus value between food and social reward may not be equivalent for a titi monkey. In order to directly compare the influence of two classes of reward, the subjective value of those rewards should be equivalent. A previous study of titi monkey food preferences showed that fruit was their most preferred class of food (Fragaszy & Mason, 1983). In rhesus macaques, food preference tests revealed that bananas are preferable to apples, and apples are preferable to carrots (Belzung & Anderson, 1986). Thus, in the current study, it is possible that the food reward we chose—banana—is a particularly palatable and preferred food item for titi monkeys and would then operate as a strong reinforcer. It would be interesting and useful in future investigations to determine food preferences prior to testing and then use the appropriate type of food based on this established scale of reward. In future studies, we could also reduce the value of the food reward by using alternative food options in order to make the value equivalent to that of the social reward.

Similarly, the subjective reward value of the return of the pair mate in our study could be low, relative to the value of the food reward. Our test subjects were habituated to short social separations during the training phase of our study, and in our colony, a subject's pair mate and/or family members are somewhat frequently removed from the home cage for short periods (minutes) in order to accommodate the specifics of research-related testing or veterinary needs, like medical treatments. After these brief separations, the animals are always promptly returned to their home cage. Thus, it is possible that the monkeys have learned over time that their pair mate will be returned to them. If this idea is true, then our subjects may perceive the temporary social separation during testing as routine and as a result, would not be motivated to engage in the task in order to work for their pair mate's return or would not find the return of the pair mate rewarding enough to consolidate their learning of the distinction between S+ and S−. In future tests, in order to increase the stimulus value in the social reward condition to match the value of a highly desirable food reward, we could increase the amount of time that the test subject is alone prior to testing.

There are a few explanations worth considering for why the food reward was more effective in our discrimination task than a social reward. One possibility is that the subjects were trained to approach and touch the shapes using food. Although banana was used during testing and peanuts were used during training, these items both belong to the same class of reward, which could have biased the behavior of our subjects in favor of the food reward during testing. Another explanation involves the concept of “preparedness” of existing behavioral systems in the titi monkey. The idea of behavioral

preparedness proposes that learning modifies innate sensorimotor and motivational systems (Timberlake, 1993), such that an organism should be more likely to learn new associations if they activate existing propensities, such as, in the current study, those systems that are involved in food acquisition and feeding. Thus, it is possible that our subjects had an increased propensity to learn our task in the food reward condition because titi monkeys use the same reaching and grasping motions that were required to select S+ to engage in feeding-related behaviors. However, titis also use reaching and grasping movements to engage in partner-directed social interactions such as grooming and mate-guarding, but Timberlake's behavioral systems approach is still worth considering in the interpretation of our results. This concept could also explain why the subjects that did reach criterion in the social reward task required more test sessions in order to successfully form the association; learning the new association is possible, but slower, because it does not activate existing behavioral systems.

Finally, it is possible, but unlikely, that differences in temporal or spatial contingencies across the two reward types could have impacted our results (Gallistel, Craig, & Shahan, 2014). Temporal contingency between the action of the individual and the outcome of its behavior is critical in reinforced learning paradigms (Flaherty, 1985). Increasing the time between the subject's correct action and the delivery of the reward has been used in studies of learning and memory to understand the maximum duration of time before a subject no longer associates their specific action with reward (for a review of delayed reinforcement on learning outcomes, see reference Lattal (2010)). Furthermore, if the delay is longer, other behavioral responses may be expressed and associated to the reinforcer (Bouton, 2007). We made every effort to immediately reveal/release/deliver the reinforcer (presenting the food reward for the subject to grab and eat, or opening the release door so that the pair mate could run into the home cage) after the subject touched S+, but we cannot control the monkeys' behavior after the reinforcer is delivered. For example, the subjects would occasionally wait to grab the banana after they touched S+, or they would wait to eat the banana after grabbing it. Also, although the pair mate always ran immediately into the home cage from the release door, we of course cannot control where in the cage the pair mate would run upon entering. On some occasions, the pair mate would run immediately into close proximity or contact with the test subject, but sometimes the pair mate would arrive in the cage at a location more distant to the test subject. However, because the return of a family member through the release door is a regular occurrence for animals in their home cage, the visual and auditory stimuli associated with the process should be an equivalent indicator of the return of their pair mate, which was initiated immediately after a correct response was given by the test subject. In all cases, the test subject immediately looked toward the reward, either to the piece of banana that appeared within reach or to the release door where their pair mate was being released. The fact that the subjects immediately attended to the reward deliveries in all tests and did not exhibit other behaviors which could be associated with the reinforcer, should resolve any potential issues of temporal contingency in the animal's understanding that their action triggered the reinforcer.

Similarly, differences in the spatial contiguity between the location of a reward can cause differences in learning (McClearn & Harlow, 1954; Murphy & Miller, 1955). In the current study, the location of the delivery of the food reward (within reach of where the subject was sitting in the trial zone) was different from the location of the delivery of the social reward (the release door at the bottom corner of the home cage). We recognize that this difference could have potentially contributed to our results. However, prior to beginning this experiment, we piloted a variety of different experimental designs to directly address the spatial difference between the reward delivery locations. Although we ultimately had to compromise on spatial contiguity, we chose the option that caused the fewest additional issues that would impair associative learning and that was the most ethologically appropriate for this species. For example, if we were to deliver the food reward at the release door, then the test subjects would have to travel toward the bottom of the cage in order to receive their reward, which introduces issues with temporal contingency as described above and also demands that the subjects approach the floor—a rare behavior for these arboreal animals, which are rarely observed on the ground (Gron, 2007). These pilot experiments directly informed our final design to ensure that the onset of all reward-related cues would be perceived by the subjects identically across conditions and immediately after a correct response was given.

Overall, this study indicates that titi monkeys can learn a two-object discrimination task, which provides a new behavioral outcome measure in our assessments of titi monkey sociality and cognition. It may be possible in future studies to combine this test of animal learning with pharmacological treatments in order to investigate the neural basis of reward learning and motivation in this species. A recent study in mice showed that social reward requires both the oxytocin and serotonin systems in the brain, acting specifically in the nucleus accumbens, which is an important region in the reward circuitry (Dölen, Darvishzadeh, Huang, & Malenka, 2013). Although the social reward was less effective in shaping titi monkey behavior, nearly half of our subjects successfully learned the discrimination task with a social reinforcer. Thus, titi monkeys can learn to associate an object with a food reward or with a social reward. It is possible that treatment with oxytocin, which is a neuropeptide that modulates several aspects of social cognition (Caldwell & Albers, 2016), could improve the behavior of titi monkeys in the social condition of this task and further contribute to our understanding of the neurobiology of social cognition.

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CONFLICTS OF INTEREST

The authors report no conflicts of interest.

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REFERENCES

Alvarado, M. C., Malkova, L., & Bachevalier, J. (2016). Development of relational memory processes in monkeys. *Developmental Cognitive Neuroscience*, *22*, 27–35. http://doi.org/10.1016/j.dcn.2016.10.007.

Anderson, J. R. (1998). Social stimuli and social rewards in primate learning and cognition. *Behavioural Processes*, *42*(2–3), 159–175.

Anzenberger, G. (1988). The pairbond in the titi monkey (Callicebus moloch): intrinsic versus extrinsic contributions of the pairmates. *Folia Primatologica; International Journal of Primatology*, *50*(3–4), 188–203.

Bales, K. L., Arias Del Razo, R., Conklin, Q. A., Hartman, S., Mayer, H. S., Rogers, F. D., . . . Wright, E. C. (2017). Titi monkeys as a novel non-human primate model for the neurobiology of pair bonding. *The Yale Journal of Biology and Medicine*, *90*(3), 373–387.

Bartal, I. B. -A., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, *334*(6061), 1427–1430. http://doi.org/10.1126/science.1210789.

Belzung, C., & Anderson, J. R. (1986). Social rank and responses to feeding competition in rhesus monkeys. *Behavioural Processes*, *12*(4), 307–316. http://doi.org/10.1016/0376-6357(86)90001-X.

Bouton M. E. (2007). *Learning and behavior: A contemporary synthesis*. Sunderland, MA: Sinauer Associates.

Bunce, J. A., Isbell, L. A., Neitz, M., Bonci, D., Surridge, A. K., Jacobs, G. H., & Smith, D. G. (2011). Characterization of opsin gene alleles affecting color vision in a wild population of titi monkeys (Callicebus brunneus). *American Journal of Primatology*,, *73*(2), 189–196. http://doi.org/10.1002/ajp.20890.

Butler, R. A. (1954). Incentive conditions which influence visual exploration. *Journal of Experimental Psychology*, *48*(1), 19–23.

Caldwell, H. K., & Albers, H. E. (2016). Oxytocin, vasopressin, and the motivational forces that drive social behaviors. *Current Topics in Behavioral Neurosciences*, *27*, 51–103. http://doi.org/10.1007/7854_2015_390.

Cubicciotti, D., & Mason, W. A. (1975). Comparative studies of social behavior in Callicebus and Saimiri: Male-female emotional attachments. *Behavioral Biology*, *16*(2), 185–197.

Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology*, *15*(6), 543–548. http://doi.org/10.1016/j.cub.2005.01.044.

Deruelle, C., Barbet, I., Dépy, D., & Fagot, J. (2000). Perception of partly occluded figures by baboons (Papio papio). *Perception*, *29*(12), 1483–1497. http://doi.org/10.1068/p3071.

Dölen, G., Darvishzadeh, A., Huang, K. W., & Malenka, R. C. (2013). Social reward requires coordinated activity of nucleus accumbens oxytocin and serotonin. *Nature*, *501*(7466), 179–184. http://doi.org/10.1038/nature12518.

Fernandez-Duque, E., Mason, W. A., & Mendoza, S. P. (1997). Effects of duration of separation on responses to mates and strangers in the monogamous titi monkey (Callicebus moloch). *American Journal of Primatology*, *43*(3), 225–237. http://doi.org/10.1002/(SICI)1098-2345(1997)43: 3<225::AID-AJP3>3.0.CO;2-Z.

Flaherty, C. F. (1985). *Animal learning and cognition*. New York City, NY: Random House.

Fragaszy, D. M. (1981). Comparative performance in discrimination learning tasks in two New World primates (Saimiri sciureus and Callicebus moloch). *Animal Learning and Behavior*, *9*(1), 127–134.

Fragaszy, D. M., & Mason, W. A. (1983). Comparisons of feeding behavior in captive squirrel and titi monkeys (Saimiri sciureus and Callicebus moloch). *Journal of Comparative Psychology*, *97*(4), 310–326.

Gallistel, C. R., Craig, A. R., & Shahan, T. A. (2014). Temporal contingency. *Behavioural Processes*, *101*, 89–96. http://doi.org/10.1016/j.beproc.2013.08.012.

Grant, D. A. (1964). Classical and operant conditioning. In A. W. Melton (Ed.), *Categories of Human Learning* (pp. 1–31). New York: Academic Press.

Gray, H., Pearce, B., Thiele, A., & Rowe, C. (2017). The use of preferred social stimuli as rewards for rhesus macaques in behavioural neuroscience. *PLoS ONE*, *12*(5), e0178048. http://doi.org/10.1371/journal.pone.0178048.

Gron, K. J. (2007, December 19). Primate Factsheets: Dusky titi (Callicebus moloch) Taxonomy, Morphology, & Ecology. Retrieved March 19, 2018, available online at: http://pin.primate.wisc.edu/factsheets/entry/dusky_titi.

Harlow, H. F. (1945). Studies in discrimination learning by monkeys; discriminations between stimuli differing in both color and form, and only in color, and only in form. *The Journal of General Psychology*, *33*, 225–235.

Harlow, H. F., & Bromer, J. A. (1938). A test apparatus for monkeys. *The Psychological Record*, *2*, 434–436.

Hawkins, R. D., & Byrne, J. H. (2015). Associative learning in invertebrates. *Cold Spring Harbor Perspectives in Biology*, *7*(5), http://doi.org/10.1101/cshperspect.a021709.

Lattal, K. A. (2010). Delayed reinforcement of operant behavior. *Journal of the Experimental Analysis of Behavior*, *93*(1), 129–139. http://doi.org/10.1901/jeab.2010.93-129.

Lucon-Xiccato, T., & Bisazza, A. (2016). Male and female guppies differ in speed but not in accuracy in visual discrimination learning. *Animal Cognition*, *19*(4), 733–744. http://doi.org/10.1007/s10071-016-0969-2.

Mason, W. A. (1974). Comparative studies of social behavior in Callicebus and Saimiri: Behavior of male-female pairs. *Folia Primatologica*, *22*, 1–8.

Mattson, B. J., Williams, S. E., Rosenblatt, J. S., & Morrell, J. I. (2003). Preferences for cocaine- or pup-associated chambers differentiates otherwise behaviorally identical postpartum maternal rats. *Psychopharmacology*, *167*(1), 1–8. http://doi.org/10.1007/s00213-002-1351-4.

Mattson, B. J., Williams, S., Rosenblatt, J. S., & Morrell, J. J. (2001). Comparison of two positive reinforcing stimuli: Pups and cocaine throughout the postpartum period. *Behavioral Neuroscience*, *115*(3), 683–694.

Mayeaux, D. J., & Mason, W. A. (1998). Development of responsiveness to novel objects in the titi monkey, Callicebus moloch. *Primates*, *39*(4), 419–431.

McClearn, G. E., & Harlow, H. F. (1954). The effect of spatial contiguity on discrimination learning by rhesus monkeys. *Journal of Comparative and Physiological Psychology*, *47*(5), 391–394.

Mendoza, S. P., & Mason, W. A. (1986). Contrasting responses to intruders and to involuntary separation by monogamous and polygynous New World monkeys. *Physiology & Behavior*, *38*(6), 795–801.

Mendoza, S. P., & Mason, W. A. (1997). Attachment relationships in new world primates. *Annals of the New York Academy of Sciences*, *807*, 203–209.

Moss, E. M., & Harlow, H. F. (1947). The role of reward in discrimination learning in monkeys. *Journal of Comparative and Physiological Psychology*, *40*(5), 333–342.

Murphy, J. V., & Miller, R. E. (1955). The effect of spatial contiguity of cue and reward in the object-quality learning of rhesus monkeys. *Journal of Comparative and Physiological Psychology*, *48*(3), 221–224.

Panksepp, J. B., & Lahvis, G. P. (2007). Social reward among juvenile mice. *Genes, Brain and Behavior*, *6*(7), 661–671. http://doi.org/10.1111/j.1601–183X.2006.00295.x.

Park, T., Okanoya, K., & Dooling, R. (1985). Operant conditioning of small birds for acoustic discrimination. *Journal of Ethology*, *3*(1), 5–9.

Pavlov I. P., (1960). In G. V. Anrep (Ed.), *Conditioned reflex: An investigation of the physiological activity of the cerebral cortex*. New York: Dover Publications, Inc.

Ridley, R. M., Bowes, P. M., Baker, H. F., & Crow, T. J. (1984). An involvement of acetylcholine in object discrimination learning and memory in the marmoset. *Neuropsychologia*, *22*(3), 253–263.

Rollin, A. R., Thaller, K. E., & Shepp, B. E. (1963). A modified wisconsin general test apparatus for rat. *American Journal of Psychology*, *76*(3), 500–&.

Seip, K. M., & Morrell, J. I. (2007). Increasing the incentive salience of cocaine challenges preference for pup- over cocaine-associated stimuli during early postpartum: Place preference and locomotor analyses in the lactating female rat. *Psychopharmacology*, *194*(3), 309–319. http://doi.org/10.1007/s00213-007-0841-9.

Skinner, B. F. (2012). How to teach animals. Scientific American Reprints, No. 423.

Tavares, M. C. H., & Tomaz, C. (2002). Working memory in capuchin monkeys (Cebus apella). *Behavioural Brain Research*, *131*(1-2), 131–137.

Thompson, T., & Sturm, T. (1965). Visual-reinforcer color, and operant behavior in Siamese fighting fish. *Journal of the Experimental Analysis of Behavior*, *8*(5), 341–344.

Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Monographs: General and Applied*, *2*(4), i–109.

Timberlake, W. (1993). Behavior systems and reinforcement – an integrative approach. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105–128. http://doi.org/10.1901/jeab.1993.60-105.

Trezza, V., Campolongo, P., & Vanderschuren, L. J. M. J. (2011). Evaluating the rewarding nature of social interactions in laboratory animals. *Developmental Cognitive Neuroscience*, *1*(4), 444–458. http://doi.org/10.1016/j.dcn.2011.05.007.

Ulloa, M., Portillo, W., Díaz, N. F., Young, L. J., Camacho, F. J., Rodríguez, V. M., & Paredes, R. G. (2017). Mating and social exposure induces an opioid-dependent conditioned place preference in male but not in female prairie voles (Microtus ochrogaster). *Hormones and Behavior*, *97*, 47–55. http://doi.org/10.1016/j.yhbeh.2017.10.015.

Wilsoncroft, W. E. (1968). Babies by bar-press: Maternal behavior in the rat. *Behavior Research Methods and Instruments*, *1*(6), 229–230. http://doi.org/10.3758/BF03208105.

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Nancy REBOUT

Testing the social complexity hypothesis: a comparative study of vocal communication in macaques

The social complexity hypothesis for communicative complexity posits that living in a complex social system requires complex communication skills. Since the complexity of a system can be measured by the amount of uncertainty it can produce, I have tested this hypothesis by comparing several primate species that differ by their level of social tolerance and the degree of uncertainty of their social interactions. First, I elaborated tools to measure three components of system complexity (diversity, flexibility, combinability) using Shannon's information theory. I developed a procedure to objectively assess diversity and flexibility using clustering algorithms and compare graded vocal systems in a common space. Then, I used this method to study the vocalisations emitted by adult females in four species of macaques: two tolerant species (Tonkean & crested macaques) and two intolerant species (Japanese & rhesus macaques). I found marked contrasts between these two pairs of species in terms of diversity and flexibility of vocal signals, with different degrees of freedom in the association between acoustic structure and context depending on the species. These results support the social complexity hypothesis by showing that animals that experience more uncertain social interactions also show a greater richness of communication signals. A wider range of expressions should help them to manage undecided social events, especially in competitive situations.

Keywords: Complexity, uncertainty, flexibility, diversity, acoustics, information theory, comparative study, social style, non-human primates.

L'hypothèse de complexité sociale pour la complexité des communications suppose que vivre dans un système social complexe requiert des compétences de communication également complexes. Comme la complexité d'un système peut se mesurer par le degré d'incertitude qu'il est capable de générer, j'ai testé cette hypothèse en comparant plusieurs espèces de primates qui diffèrent par leur niveau de tolérance sociale et le degré d'incertitude de leurs interactions sociales. J'ai d'abord élaboré les outils nécessaires pour mesurer trois composantes de la complexité des systèmes (diversité, flexibilité, combinabilité) à partir de la théorie de l'information de Shannon. J'ai développé une procédure pour évaluer objectivement la diversité et la flexibilité à l'aide d'analyses en clusters et, ainsi, comparer des systèmes vocaux gradués dans un espace commun. J'ai ensuite utilisé cette méthode pour étudier les vocalisations émises par les femelles adultes chez quatre espèces de macaque : deux espèces tolérantes (macaques de Tonkean & macaques à crête) et deux espèces intolérantes (macaques japonais & macaques rhésus). J'ai trouvé des différences marquées entre ces deux paires d'espèces en termes de diversité et de flexibilité des signaux vocaux, avec différents degrés de liberté dans l'association entre structure acoustique et contexte en fonction des espèces. Ces résultats viennent appuyer l'hypothèse de la complexité sociale en montrant que les animaux ayant des interactions sociales plus incertaines font également preuve d'une plus grande richesse dans leurs signaux de communication. Un spectre d'expression plus large devrait les rendre apte à faire face à des événements sociaux indécis, en particulier dans les situations de compétition.

Mots-clés : Complexité, incertitude, flexibilité, diversité, acoustique, théorie de l'information, étude comparative, style social, primates non humains.