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Camille Vitet

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

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Unité de recherche : Centre d'Écologie Fonctionnelle et Évolutive

Effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale du zèbre des plaines en contexte de prédation

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Le 1^{er} décembre 2020

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ABSTRACT

In social species, costs and benefits of group living are numerous and dynamic, and the balance between them is a key determinant of group size. Group size is a component of sociality which can have important effects on the behaviour of individuals, their demographic parameters and their social dynamic (intergroup movements of individuals, associations between groups). However, these effects remain poorly understood. In this thesis, I explore the effect of group size on the behaviour, demography and social dynamic of plains zebras *Equus quagga* in the wild populations of Hwange National Park (HNP, Zimbabwe) and Hluhluwe-iMfolozi Park (HiP, South Africa). In the first chapter, I show that, in HNP, group size has little effect on individual vigilance and foraging, and has no significant effect on the survival of individuals, suggesting that dilution and detection effects do not matter behaviourally and demographically in this population. In the second chapter, I show that the probability of stallion turnover increases with the number of reproductive females in harems in HNP, but that these stallion turnovers do not affect foal survival. This suggests that, if infanticide by males occurs in wild plains zebras, this should be extremely rare and has no important consequences for foal survival at the population level. Finally, in the third chapter, I show that the number of reproductive females in harems has no effect on the probability for harems to be alone or with other harems. However, harems with many reproductive females seem to be found less often near bachelors (although significant uncertainty remains). This suggests that harems including many reproductive females may seek to avoid bachelors, and actually seem to have more success in doing it in HiP where vegetation is overall more closed than in HNP. Accordingly, the probability of stallion turnover does not increase with the number of reproductive females in harems in HiP. Overall, this thesis questions the functioning of the dilution effect and highlights the importance of considering the potential regulatory effect of social dynamics on populations, through their effect on the spatial distribution of groups.

KEYWORDS: sociality, behaviour, demography, social dynamic, ungulate, predation

RESUME

Chez les espèces sociales, les coûts et bénéfices de la vie en groupe sont nombreux et dynamiques, et la balance entre ces derniers est un déterminant clé de la taille des groupes. La taille de groupe est un composant de la socialité qui peut avoir d'importants effets sur le comportement des individus, leurs paramètres démographiques et leur dynamique sociale (mouvements intergroupes des individus, associations entre groupes). Cependant, ces effets restent mal compris. Dans cette thèse, j'explore l'effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale du zèbre des plaines *Equus quagga* dans les populations sauvages du Parc National de Hwange (HNP, Zimbabwe) et du Parc de Hluhluwe-iMfolozi (HiP, Afrique du Sud). Dans le premier chapitre, je montre qu'à HNP la taille de groupe a peu d'effet sur la vigilance individuelle et l'acquisition des ressources, et n'a pas d'effet significatif sur la survie des individus, ce qui suggère que les effets de dilution et de détection importent peu sur le plan comportemental et démographique dans cette population. Dans le second chapitre, je montre que la probabilité qu'il y ait un changement d'étalon au sein des harems augmente lorsque le nombre de femelles reproductrices dans les harems augmente à HNP, mais que ces changements d'étalon n'affectent pas la survie des poulains. Ainsi, si le comportement d'infanticide par les mâles existe chez le zèbre des plaines en milieu sauvage, il devrait être très rare et ne pas avoir d'impact important sur la survie des poulains à l'échelle de la population. Enfin, dans le troisième chapitre, je montre que le nombre de femelles reproductrices dans les harems n'a pas d'effet sur la probabilité des harems à être observés seuls ou avec d'autres harems. En revanche, les harems comprenant davantage de femelles reproductrices semblent être moins souvent observés avec des groupes de mâles célibataires (bien que des incertitudes demeurent). Cela suggère que les harems comprenant beaucoup de femelles reproductrices pourraient éviter de s'associer avec les mâles célibataires, et semblent mieux réussir à les éviter à HiP où la végétation est globalement plus fermée qu'à HNP. De ce fait, la probabilité qu'il y ait un changement d'étalon au sein des harems n'augmente pas avec le nombre de femelles reproductrices dans les harems à HiP. Globalement, cette thèse remet en question le fonctionnement de l'effet de dilution et souligne l'importance de considérer l'effet régulateur potentiel des dynamiques sociales sur les populations, à travers leur effet sur la distribution spatiale des groupes.

MOTS CLES : socialité, comportement, démographie, dynamique sociale, ongulé, prédation

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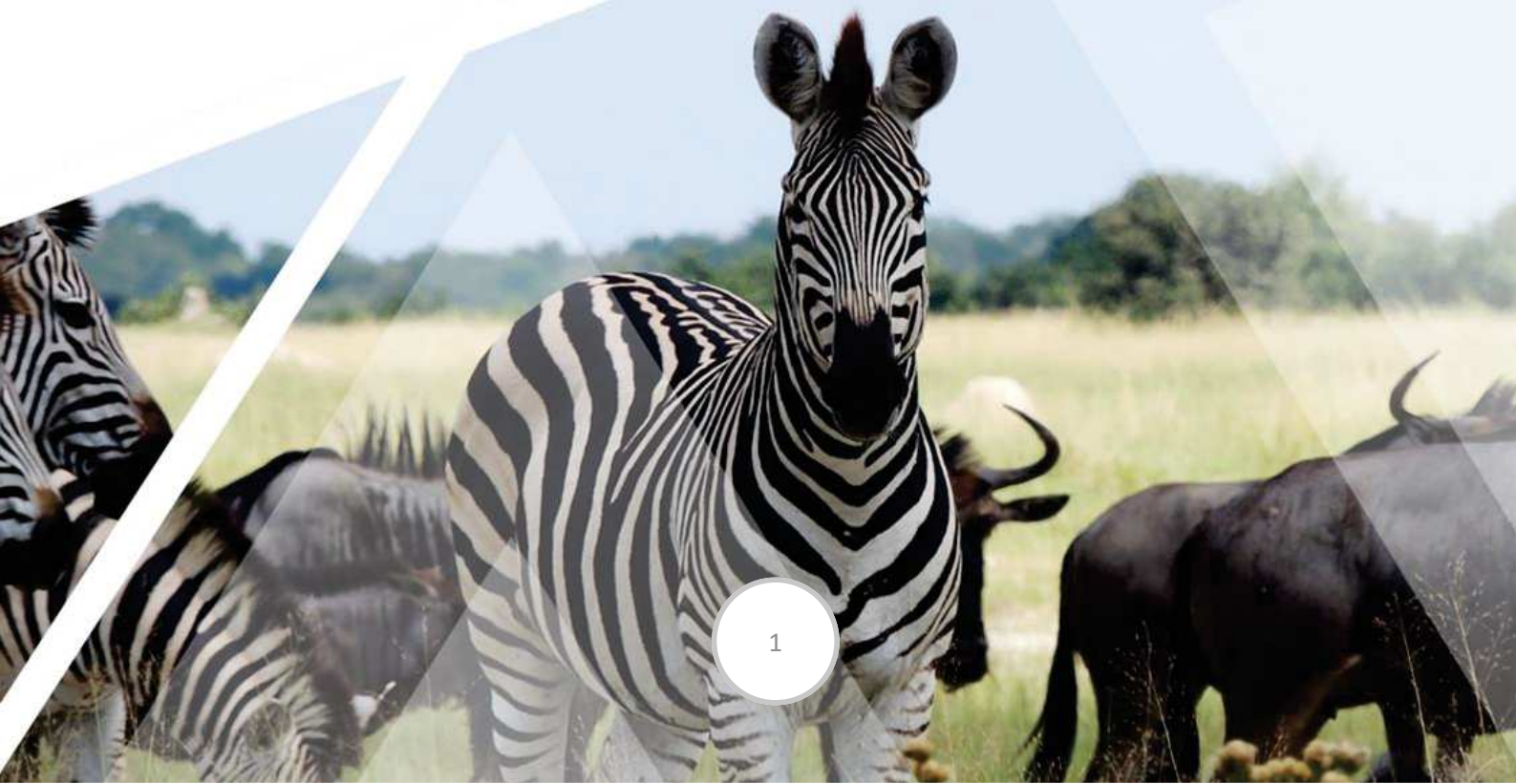
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INTRODUCTION



CONTEXTE

La dynamique des populations est une branche de l'écologie qui étudie comment et pourquoi la taille des populations varie dans le temps et l'espace (Royama 1992, Turchin 2003). Ce champ disciplinaire a pour but de documenter les fluctuations d'effectifs (nombre d'individus) au sein des populations et de déterminer les mécanismes sous-jacents responsables des variations observées. En ce sens, elle fournit des outils utiles à la gestion et à la conservation des espèces. Les premières recherches en dynamique des populations sont apparues à partir des années 1920 avec les travaux d'Elton (1924), Lotka (1925), Volterra (1926), et Nicholson (1933). Historiquement, ces recherches étaient centrées sur l'étude des tailles des populations et des fluctuations de ces dernières au cours du temps. A ce niveau global, cela permet de déterminer la tendance d'une population (si celle-ci croît, décline ou est proche de l'extinction) mais ne permet pas d'identifier les mécanismes sous-jacents. Par la suite, de nombreuses recherches se sont intéressées à l'étude des paramètres démographiques et des facteurs influençant ces derniers. L'étude des paramètres démographiques que sont les paramètres de croissance (taux de natalité et d'immigration) et de décroissance (taux de mortalité et d'émigration) s'inscrit dans le domaine de la démographie. L'estimation de ces paramètres et l'identification des potentiels facteurs les influençant sont essentiels à une bonne compréhension de la dynamique d'une population. En effet, cette dernière résulte de la capacité de chaque individu à survivre, se disperser et se reproduire, et le taux de chacun de ces processus va donc avoir un impact sur la dynamique de la population (Tuljapurkar and Caswell 1997). Ainsi, l'étude d'une population peut se faire à trois niveaux (Gaillard 1988): (i) l'étude des tailles des populations, (ii) l'étude des paramètres démographiques des individus (survie, reproduction, dispersion), et (iii) l'étude des facteurs influençant ces paramètres.

Le lien entre les paramètres démographiques des individus et la dynamique des populations a été documenté chez de nombreuses espèces de vertébrés, comme chez les oiseaux (Juillard 2004, Waugh et al. 2015, Genovart et al. 2018), les ongulés (Gaillard et al. 1998, 2000), les primates non humains (Mandujano and Escobedo-Morales 2008, Lawler 2011), et les rongeurs (Oli and Armitage 2004, Krebs 2013). Ces études ont mis en évidence les impacts relatifs que peuvent avoir les variations des taux de survie et de reproduction des individus sur la dynamique des populations.

La majorité des facteurs ayant une influence sur les paramètres démographiques des individus ont également été identifiés. En fonction de leur âge, sexe et statut, les taux de survie et de reproduction des individus peuvent varier. Par exemple, un individu âgé aura généralement

une survie et/ou un succès reproducteur plus faible qu'un individu plus jeune, comme cela a été montré chez les primates non humains (Strum and Western 1982), les rongeurs (Farand et al. 2002, Berger et al. 2016), les chiroptères (Culina et al. 2017) et les ongulés (Jorgenson et al. 1997, Loison et al. 1999, Grange et al. 2004). La densité de population peut aussi avoir un effet sur les paramètres démographiques des individus (Nicholson 1933, Allee et al. 1949, Eberhardt 1977, 2002, Sinclair 1989, Den Boer et al. 1996). Cet effet a été exploré chez de nombreuses espèces comme par exemple chez les grands herbivores (voir références dans Bonenfant et al. 2009), les oiseaux (Lieske et al. 2000, Krüger 2007), les insectes (Nowicki et al. 2009) et les primates non humains (Hernández-Pacheco et al. 2013). Le climat, les précipitations, la température et la disponibilité en ressources alimentaires sont autant de facteurs environnementaux qui peuvent aussi influencer sur la capacité des individus à survivre et se reproduire. Des relations entre les conditions environnementales et les paramètres démographiques des individus ont été documentées chez diverses espèces de rongeurs (Russell and Ruffino 2012, Rézouki et al. 2016, Lock and Wilson 2017, Selonen et al. 2019), d'oiseaux (Moss et al. 2001, Sandvik et al. 2012, Monadjem et al. 2012, Jenouvrier et al. 2018) et d'ongulés (Loison and Langvatn 1998, Mduma et al. 1999, Weladji et al. 2002, Mysterud et al. 2003, Ciach and Pęksa 2018). Les interactions interspécifiques peuvent également avoir un effet sur les paramètres démographiques des individus. Plusieurs études ont par exemple démontré un rôle important des relations prédateur-proie dans le déclin de certaines populations de proies, notamment chez les ongulés (Harrington et al. 1999, Tambling and Du Toit 2005, Wittmer et al. 2005, Festa-Bianchet et al. 2006, Nilsen et al. 2009) et les oiseaux (Roos et al. 2018). Les prédateurs n'affectent pas seulement la dynamique des populations de proies en tuant des individus : ils peuvent aussi impacter leurs proies de manière indirecte via des effets sur leur physiologie (ex : stress) ou leur comportement (ex : changement d'utilisation de l'espace, augmentation de la vigilance) (Lima 1998, Clinchy et al. 2004, Creel and Christianson 2008, Sheriff et al. 2009, McCauley et al. 2011). Ces effets indirects de la prédation ont été documentés chez les insectes (Peckarsky et al. 1993, Schmitz et al. 1997, Teichroeb et al. 2014), les amphibiens (Peacor 2002), les oiseaux (Dudeck et al. 2018) et les mammifères (Barnier et al. 2014, Dulude-de Broin et al. 2020). Les relations hôte-parasite peuvent aussi affecter les paramètres démographiques des individus parasités (Brown and Brown 2004, Hillegass et al. 2010).

Les ajustements comportementaux sont l'un des mécanismes clés du lien entre ces facteurs et les paramètres démographiques des individus. L'écologie comportementale est la discipline scientifique qui a pour objectif de comprendre comment le comportement des animaux est adapté à l'environnement dans lequel ils vivent (Davies et al. 2012). Cette discipline a

longtemps été étudiée séparément de la dynamique des populations, mais de plus en plus d'études explorent désormais le lien entre le comportement des individus et la dynamique des populations, de manière théorique (ex : Ives and Dobson 1987, Sutherland 1996, Fryxell and Lundberg 1998) et empirique (ex : Anholt 1997, Levin et al. 2000, Coolen et al. 2007, Green et al. 2019). Des travaux de recherche ont par exemple montré des effets des comportements spatiaux (ex : utilisation de l'espace, sélection de l'habitat) sur la survie et la reproduction des individus, notamment chez les ongulés (Forrester et al. 2015, Losier et al. 2015, Lafontaine et al. 2017) et les oiseaux (voir références dans Piper 2011). D'autres études ont mis en évidence des effets des comportements d'évitement des prédateurs (Sansom et al. 2009), des comportements de réponse face à l'attaque d'un prédateur (Lingle and Pellis 2002), des comportements d'alimentation (Authier et al. 2012), des comportements de vigilance (FitzGibbon 1989, Watson et al. 2007, Sansom et al. 2009) et de la personnalité (voir références dans Smith and Blumstein 2008, Moiron et al. 2020) sur les paramètres démographiques des individus. Les études combinant des données comportementales et des mesures de survie et de reproduction sur le long terme restent cependant rares, et l'effet du comportement des individus sur leur survie et leur reproduction reste mal compris.

Les facteurs énoncés précédemment jouent un rôle important sur la faculté des individus à survivre et se reproduire, et il est aujourd'hui reconnu que tous ces facteurs n'agissent pas seuls et que la dynamique des populations est déterminée par leurs interactions (Benton et al. 2006, Bonenfant et al. 2009, Oro 2013). En effet, des relations complexes entre ces différents facteurs existent. Par exemple, des effets interactifs du climat et de la densité sur les paramètres démographiques des individus ont été montrés chez les oiseaux (Grøtan et al. 2009, Fay et al. 2015, Sandvig et al. 2017) et les ongulés (Sæther 1997, Coulson et al. 2000, 2001, Georgiadis et al. 2003, Solberg et al. 2008, Brown 2011). D'autres interactions ont aussi été mises en évidence, comme par exemple des interactions entre conditions climatiques et prédation (Hebblewhite 2005, Fargallo et al. 2009) et des interactions entre âge, sexe et densité (Jorgenson et al. 1997, Bonenfant et al. 2002).

Un comportement supplémentaire pouvant affecter les paramètres démographiques des individus est la socialité. Nous avons vu précédemment que le comportement des individus peut avoir d'importantes implications sur leur survie et leur reproduction. Or, la vie en groupe et les caractéristiques des systèmes sociaux tels que la taille des groupes peuvent induire des modifications comportementales et donc avoir un impact sur les paramètres démographiques des individus et sur la dynamique des populations.

LA SOCIALITE

La socialité désigne la tendance des individus à vivre en groupe (Alexander 1974), un groupe étant composé de plusieurs individus d'une même espèce vivant ensemble sur une période de temps donnée et interagissant entre eux à un degré supérieur qu'avec d'autres conspécifiques (Wilson 1975). Au sein du règne animal, un grand nombre de systèmes sociaux existent (Crook et al. 1976). Leur diversité peut être décrite par trois composantes (Kappeler and Schaik 2002) : (i) l'organisation sociale qui fait référence à la taille des groupes, leur composition et leur cohésion, (ii) le système d'accouplement qui décrit quels individus mâles et femelles s'accouplent dans chaque groupe (composante sociale) et les conséquences de ces accouplements en termes de reproduction (composante génétique), et (iii) la structure sociale qui concerne les interactions sociales et les relations entre individus.

On distingue trois niveaux dans la structure sociale des systèmes sociaux : (i) les interactions sociales qui sont définis comme étant « des comportements par lesquels les individus agissent les uns sur les autres et s'influencent », les relations sociales qui représentent « une succession d'interactions entre partenaires qui se connaissent », et les réseaux sociaux qui impliquent « l'ensemble des relations sociales existant entre les membres d'un groupe » (Darmaillacq and Lévy 2019).

Les systèmes sociaux peuvent être placés sur un gradient de socialité allant de l'individu solitaire à des groupes sociaux complexes, le passage à un degré de socialité supérieur étant marqué par l'apparition de paramètres de complexité croissante, tels que l'apparition des comportements parentaux ou la spécialisation des tâches par castes (Aron and Passera 2000) (Tableau 1).

Tableau 1. Classification et définition des degrés de socialité (adaptée de Berger 2015)

Degrés de socialité			Définitions	
Solitaire			<ul style="list-style-type: none"> . Pas de formation de groupes . Pas d'interactions entre adultes sauf pendant la période de reproduction 	
Grégaire			<ul style="list-style-type: none"> . Formation de groupes . Attraction réciproque des individus (interattraction) . Pas d'interactions entre adultes . Chez certaines espèces, les individus sont grégaires seulement pendant la période de reproduction . Soins allomaternels possibles 	
Colonial			<ul style="list-style-type: none"> . Formation de groupes par paires en période de reproduction (parfois pour la vie) . Peu d'interactions entre paires 	
Social	Tous les individus se reproduisent	Sans soins alloparentaux	<ul style="list-style-type: none"> . Vie en groupe . Interactions coopératives entre individus . Chevauchement des générations 	
		Avec soins alloparentaux	<ul style="list-style-type: none"> . Soins alloparentaux 	
		Reproduction communautaire	<ul style="list-style-type: none"> . Synchronisation de la reproduction et coopération équitable de tous les individus pour les soins parentaux 	
	Quelques individus se reproduisent	Reproduction coopérative	Réversible	<ul style="list-style-type: none"> . Monopolisation de la reproduction par le couple dominant . Reproduction et dispersion retardées pour les subordonnés . Les subordonnés procurant les soins alloparentaux sont appelés <i>helpers</i>
			Eusocial	<ul style="list-style-type: none"> . Spécialisation des tâches par castes : une ou quelques femelles se reproduisent et les subordonnés sont stériles

De nombreuses raisons évolutives ont été avancées pour expliquer la diversité des systèmes sociaux. Trois principales pressions écologiques ont été proposées comme déterminants majeurs de l'évolution de la socialité : le risque de prédation, l'acquisition des ressources alimentaires et l'accès à la reproduction (Majolo and Huang 2018). Chacune de ces pressions écologiques va procurer des bénéfices et des coûts aux individus vivant en groupe (Krause and Ruxton 2002, Majolo et al. 2008). Dans la section suivante, je présente les bénéfices et les coûts associés à chacune de ces pressions écologiques, ainsi que les effets de la taille de groupe sur le comportement des individus et la dynamique sociale des groupes (mouvements intergroupes des individus, associations entre groupes), et les différents compromis comportementaux que les individus doivent effectuer afin de maximiser leur survie et leur reproduction.

BENEFICES ET COUTS DE LA VIE EN GROUPE ET MODIFICATIONS COMPORTEMENTALES ASSOCIEES

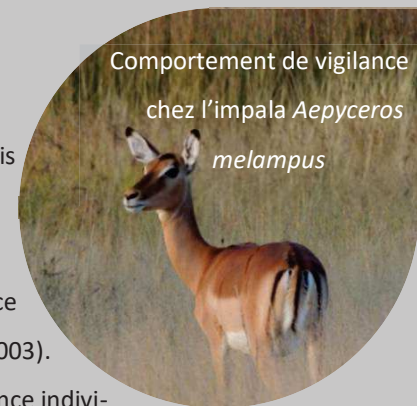
Bénéfices et coûts de la vie en groupe liés au risque de prédation

Dans un contexte de prédation, vivre en groupe permet aux proies d'être mieux protégées contre les prédateurs. Ce bénéfice est permis via plusieurs effets. Tout d'abord, il y a l'effet de détection qui traduit l'idée que plus il y a d'individus dans un groupe et plus la détection d'un prédateur en approche sera efficace. En effet, dans les grands groupes, davantage d'individus sont disponibles pour scanner l'environnement, chaque individu du groupe pouvant alors réduire son niveau de vigilance individuelle tout en ayant la même probabilité de détecter un prédateur (Pulliam 1973, Lima 1995). La présence de congénères dilue aussi le risque pour chaque individu du groupe d'être prédaté lors d'une attaque, à condition que le taux d'attaque n'augmente pas avec la taille de groupe et que le prédateur ne prélève qu'une seule proie à la fois : c'est l'effet de dilution (Bertram 1978, Lehtonen and Jaatinen 2016). Les effets de dilution et de rencontre (lorsqu'un prédateur a moins de chance de rencontrer un seul groupe de proies que de rencontrer des individus solitaires et dispersés) sont généralement combinés sous le terme d'*attack abatement* (Turner and Pitcher 1986). Enfin, il y a l'effet de confusion qui traduit l'idée que la capacité d'un prédateur à différencier et suivre une proie est réduite lorsque cette proie fait partie d'un groupe, conduisant à une réduction du ratio attaque/capture pour le prédateur (Miller 1922, Jeschke and Tollrian 2007). Cette sécurité accrue dans les grands groupes peut entraîner des modifications comportementales chez les individus, comme par exemple une diminution de la vigilance (anti-prédateur) individuelle à mesure que la taille de groupe augmente (Box. 1). Les grands groupes bénéficiant d'une meilleure protection contre les prédateurs peuvent aussi modifier leur utilisation de l'espace en profitant de cette sécurité accrue pour explorer et utiliser des zones plus

risquées qui sont aussi souvent plus riches en ressources (Fortin et al. 2009, Patin 2018). La sécurité accrue dont bénéficient les grands groupes peut aussi avoir un impact sur la dynamique sociale des groupes, notamment sur les associations entre les différents groupes sociaux. Par exemple, chez les espèces vivant au sein de sociétés multi-niveaux qui sont des sociétés dans lesquelles les individus appartiennent à une unité sociale stable et s'associent temporairement avec d'autres groupes de conspécifiques (Grueter et al. 2017b), des études ont mis en évidence que les associations temporaires entre groupes permettent à ces derniers d'abaisser leur risque de prédation (Rubenstein 1986, Schreier and Swedell 2009, Tong et al. 2015, Lin et al. 2020).

Box 1. Taille de groupe et vigilance anti-prédateur

Le comportement de vigilance a plusieurs fonctions : il permet de détecter des prédateurs (vigilance anti-prédateur) (Caro 2005), mais aussi de surveiller les autres membres du groupe afin de limiter la compétition et les agressions, d'acquérir des informations sur la localisation des ressources ou de chercher des partenaires (vigilance sociale) (Treves 2000, Beauchamp 2001, Beauchamp and Ruxton 2003).



Dans le cas de la vigilance anti-prédateur, la diminution de la vigilance individuelle à mesure que la taille de groupe augmente (*group-size effect on vigilance*) est une relation qui a été observée dans de nombreux taxa (Elgar 1989, Quenette 1990, Lima and Dill 1990), notamment chez les mammifères (Underwood 1982, Quenette and Gerard 1992, Burger and Gochfeld 1992, Burger et al. 2000, Pays et al. 2007c, 2012, Périquet et al. 2012, Favreau et al. 2018) et les oiseaux (Martella et al. 1995, Fernandez et al. 2003, Wang et al. 2015). Cependant, un nombre croissant d'études obtiennent des résultats qui ne soutiennent pas cette relation (Treves 2000, Laundre et al. 2001, Beauchamp 2008, Périquet et al. 2017), ce qui pourrait être expliqué par l'existence de stratégies anti-prédateur alternatives comme le fait de se regrouper (Creel et al. 2014) ou d'ajuster son utilisation de l'espace (Creel and Creel 2015, Patin et al. 2019). Les résultats des études sur le lien entre taille de groupe et vigilance individuelle sont donc mixtes. Il en est de même pour le lien entre taille de groupe et vigilance collective. A mesure que la taille de groupe augmente, on observe généralement une augmentation de la vigilance collective (pourcentage de fois où au moins un individu du groupe est vigilant; Lima 1995). L'augmentation de la vigilance collective avec la taille de groupe a été documentée dans de nombreux travaux (Bertram 1980, Ebensperger et al. 2006, Pays et al. 2007c, 2012, Pays and Jarman 2008, Wang et al. 2015) mais les études ne montrant pas cette relation existent (Quenette and Gerard 1992, Fernandez et al. 2003) et le lien entre taille de groupe et vigilance collective est parfois complexe : chez le kangourou géant *Macropus giganteus*, Pays et al. (2007b) ont montré que la vigilance collective augmente avec la taille de groupe pour les groupes de 6 individus et moins, mais diminue avec la taille de groupe pour les groupes de plus de 6 individus. Les résultats des études qui se sont intéressées à l'effet de la taille de groupe sur la vigilance collective sont donc aussi hétérogènes.

Vivre en groupe dans un contexte de prédation peut aussi être coûteux. En effet, les grands groupes de proies peuvent être plus visibles (Vine 1973) et l'augmentation du taux d'attaque par des prédateurs avec la taille des groupes de proies est un coût majeur de la socialité pour de nombreux animaux (Creel & Creel, 2002; Cresswell, 1994; Krause & Godin, 1995; Lindström, 1989; voir cependant Treherne and Foster 1982, Fitzgibbon 1990).

Bénéfices et coûts de la vie en groupe liés à l'acquisition des ressources alimentaires

En termes d'acquisition des ressources alimentaires, s'alimenter en groupe peut être bénéfique (Clark and Mangel 1986). Par exemple, les prédateurs peuvent augmenter leur succès d'attaque en chassant en groupe, comme c'est le cas chez le lion *Panthera leo* (Van Orsdol 1984) et le loup *Canis lupus* (MacNulty et al. 2014). Pour les proies, s'alimenter en groupes peut être bénéfique via le transfert d'information sur la localisation de patches de ressources, particulièrement lorsque la localisation des ressources dans l'environnement est variable (Rodman 1988, Templeton and Giraldeau 1995, 1996, Gager 2019). Les grands groupes ont aussi plus de chance de supplanter d'autres groupes et d'accéder à leurs ressources, comme cela a été montré par exemple chez les loups (Cassidy et al. 2015) et plusieurs espèces de primates non humains (Majolo et al. 2020). Nous avons aussi vu qu'une augmentation de la taille des groupes conduit généralement à une réduction de la vigilance individuelle (Box. 1). Cette diminution de la vigilance peut permettre aux individus de consacrer une plus grande partie de leur budget temps à l'alimentation comme cela a été montré chez les ongulés (Burger et al. 2000, Isvaran 2007, Barnier et al. 2016) et les oiseaux (Boland 2003, Fernandez et al. 2003, Beauchamp 2008). Cependant, il est important de noter que des relations négatives (Molvar and Bowyer 1994, Focardi and Pecchioli 2005), non linéaires (Heinsohn 1987, Hintz and Lonzarich 2018) et des absences de relation (Stacey 1986, Cresswell 1994, Périquet et al. 2017) entre taille de groupe et acquisition des ressources alimentaires ont aussi été documentées.

S'alimenter en groupe peut aussi s'avérer coûteux et conduire à une augmentation de la compétition intragroupe pour l'accès aux ressources alimentaires (Clark and Mangel 1986). Par exemple, cela peut conduire à du kleptoparasitisme, qui désigne le fait de se faire voler sa nourriture par un conspécifique ou un individu d'une autre espèce (Brockmann and Barnard 1979, Iyengar 2008). De plus, la compétition intra-groupe accrue pour l'accès aux ressources dans les grands groupes peut conduire à une augmentation des interactions agonistiques entre les membres du groupe, comme cela a été montré chez les ongulés (Molvar and Bowyer 1994 ; mais voir Risenhoover and Bailey 1985, Fortin et al. 2004). Vivre en groupe peut aussi conduire à de la pseudo-interférence. En effet, les grands groupes épuisent généralement les ressources plus

rapidement, chaque individu obtenant une plus petite part des ressources, ce qui peut conduire ces derniers à exploiter des zones moins profitables et induire une baisse du taux d'acquisition des ressources (Free et al. 1977, Cresswell 1998). Ces coûts liés à l'acquisition des ressources peuvent aussi entraîner des modifications comportementales en termes d'utilisation de l'espace : les grands groupes pourraient avoir besoin de voyager sur de plus longues distances et d'élargir leurs domaines vitaux pour subvenir à leurs besoins énergétiques (Majolo et al. 2008).

Bénéfices et coûts de la vie en groupe liés à l'accès à la reproduction

En termes d'accès à la reproduction, la vie en groupe procure quelques avantages. Elle permet de faciliter l'accès à des partenaires potentiels et crée une opportunité de pouvoir choisir parmi ces derniers (Ward and Webster 2016). En effet, chez les espèces ne vivant pas en groupe, les individus doivent chercher un partenaire ou s'accoupler de manière opportuniste quand ils en rencontrent un, alors que chez les espèces vivant en groupe, les individus choisissent simplement un partenaire parmi les membres de leur groupe. Chez certaines espèces, les leks (aires de parade et de reproduction) permettent aux mâles dominants de maximiser leur accès à la reproduction en s'engageant dans des comportements de parades (ex : combats avec d'autres mâles, vocalisations) qui leur permettent de démontrer leur force physique et leur qualité génétique aux femelles qui visitent les leks dans le but de se reproduire (McComb 1991, Apollonio et al. 1992). Pour les femelles, les leks leur permettent d'évaluer la force et la qualité de chaque mâle, et offrent une excellente opportunité de choisir leur partenaire (Jiguet and Bretagnolle 2001, Chargé et al. 2010).

En termes de coûts, la vie en groupe peut induire de la compétition entre les individus pour avoir accès à un partenaire, à un territoire ou à des ressources pour leurs progénitures (Clutton-Brock 2016, chapitre 8). Par exemple, chez de nombreux mammifères sociaux, la compétition entre les femelles pour avoir accès à la reproduction est courante (Silk 2007, Stockley and Bro-Jørgensen 2011, Nelson-Flower et al. 2013) et conduit parfois à une suppression de la reproduction pour certaines d'entre elles (Clutton-Brock et al. 2008, Beehner and Lu 2013). Les individus dans les grands groupes peuvent aussi être davantage exposés à des risques d'infanticides par les mâles (lorsqu'un mâle adulte conspécifique tue un jeune non apparenté encore dépendant de sa mère). En effet, chez certaines espèces, il a été montré que les changements de mâles (remplacement du mâle reproducteur d'un groupe par un autre mâle) au sein des groupes de femelles sont plus fréquents dans les grands groupes de femelles que dans les petits groupes (Dunbar 1984, Crockett and Janson 2000, Steenbeek and Van Schaik 2001, Teichroeb et al. 2012) et que ces changements de mâle conduisent généralement à une

augmentation du risque d'infanticide (Bertram 1975, Butynski 1982, 1990, Packer and Pusey 1983, Packer et al. 1988). Face à ce risque, les femelles peuvent mettre en place des comportements coopératifs pour s'aider dans la défense de leurs petits contre les mâles infanticides (Smuts and Smuts 1993, Palombit 2015). A ces modifications comportementales peuvent s'ajouter des modifications en termes de dynamique sociale : chez certaines espèces vivant en sociétés multi-niveaux, il a été montré que les groupes reproducteurs s'associent entre eux pour réduire le risque de harcèlement des femelles par les *bachelors* (mâles célibataires) et le risque de changement de mâle (Rubenstein 1986, Rubenstein and Hack 2004, Pappano et al. 2012).

Autres coûts et bénéfices de la vie en groupe

En dehors des coûts et bénéfices liés au risque de prédation, à l'acquisition des ressources alimentaires et à l'accès à la reproduction, d'autres bénéfices de la vie en groupe existent. Vivre en groupe peut notamment permettre de réduire les coûts énergétiques liés à la conservation de la chaleur (Gilbert et al. 2010) ou aux déplacements dans l'eau ou l'air (Fish 1999, Weimerskirch et al. 2001). D'autres coûts liés à la vie en groupe existent aussi : vivre en groupe peut faciliter la transmission et la persistance de parasites ou de maladies (Patterson and Ruckstuhl 2013), et rendre plus difficile la synchronisation d'activités pour maintenir la cohésion des groupes (Wilson et al. 1986, Ruckstuhl 1998; mais voir Beauchamp 1992).

Les compromis comportementaux

Pour maximiser sa survie et sa reproduction, chaque individu doit répartir son temps entre diverses activités, telles que l'évitement des prédateurs et la recherche de ressources (nourriture, partenaire) et doit donc faire des compromis (Fraser and Hutingford 1986, Lima and Dill 1990).

Chez les proies, l'un des compromis majeurs se situe entre l'évitement des prédateurs et l'acquisition des ressources (*food-safety trade-off*; Houston et al. 1993, Brown 1999, Bonter et al. 2013). Les proies peuvent augmenter leur niveau de vigilance afin de détecter plus facilement les prédateurs, mais en contrepartie, cela conduit généralement à une diminution du taux d'acquisition des ressources alimentaires (Laundre et al. 2001, Fritz et al. 2002, Cowlshaw et al. 2004, Fortin et al. 2004). De même, l'utilisation de zones moins risquées permet de réduire le risque de prédation, mais ces dernières sont généralement moins profitables en termes de ressources alimentaires (Cowlshaw 1997, Williams and Flaxman 2012). Vivre en groupe peut également offrir une meilleure protection contre les prédateurs mais cela peut induire une augmentation de la compétition entre les membres du groupe pour l'accès aux ressources alimentaires (Krause and Ruxton 2002).

Certains individus doivent aussi faire un compromis entre protection contre les prédateurs et reproduction. Par exemple, chez les espèces sociales dont les sociétés sont composées de groupes unimâle- ou multimâles-multifemelles, et de groupes de *bachelors*, les associations temporaires entre groupes peuvent diminuer le risque de prédation mais aussi augmenter les risques de harcèlement des femelles, de changement de mâle, et d'infanticide que posent les *bachelors* pour les groupes reproducteurs (Dunbar 1984, Packer et al. 1988, Borries 1997, Crockett and Janson 2000). De nombreux autres compromis existent, comme par exemple le compromis entre alimentation et accouplement (Griffiths 1996, Köhler et al. 2011), gain énergétique et parasitisme (Norris 1999, Lienhard et al. 2010), ou protection du nid et alimentation (Komdeur and Kats 1999).

Pour les espèces sociales, les bénéfices et coûts liés à la vie en groupe sont donc nombreux et dynamiques. La balance entre ces derniers est un déterminant clé de la taille des groupes qui, comme nous l'avons vu, peut à son tour induire des modifications comportementales chez les individus et avoir un impact sur la dynamique sociale des groupes. Il est donc attendu que la taille de groupe affecte aussi les paramètres démographiques des individus.

TAILLE DE GROUPE ET PARAMETRES DEMOGRAPHIQUES

Comme les coûts et les bénéfices de la vie en groupe varient en fonction des espèces et des conditions environnementales, différentes formes de relation entre la taille de groupe et la survie et la reproduction des individus ont été proposées (Sibly 1983, Krause and Ruxton 2002). Généralement, on s'attend à ce que la survie et la reproduction des individus augmentent avec la taille de groupe en raison de la réduction du risque de prédation et/ou de l'augmentation de l'approvisionnement en ressources jusqu'à ce que les coûts d'une compétition accrue au sein du groupe en compensent les avantages (Sibly 1983, Markham et al. 2015). Chez certaines espèces, on peut également s'attendre à une baisse du taux de survie des jeunes et du succès reproducteur des femelles à mesure que la taille de groupe augmente, puisque, comme évoqué précédemment, des études ont montré que les changements de mâle sont plus fréquents dans les groupes comprenant un grand nombre de femelles reproductrices (en âge de se reproduire) (Dunbar 1984, Crockett and Janson 2000, Steenbeek and Van Schaik 2001, Teichroeb et al. 2012), ce qui peut conduire à une augmentation des risques d'infanticides dans les grands groupes (Bertram 1975, Butynski 1982, 1990, Packer and Pusey 1983, Packer et al. 1988). A l'inverse, chez les espèces à reproduction coopérative, on peut s'attendre à un effet positif de la taille de groupe sur la reproduction et la survie des individus puisqu'un effet positif du nombre d'*helpers* sur le

succès reproducteur des individus dominants et la survie des juvéniles a été documenté chez plusieurs espèces (Clutton-Brock et al. 2001, Hayes and Solomon 2004, Koenig and Dickinson 2016 ; voir cependant Cockburn 1998).

Les coûts et bénéfices associés aux différentes tailles de groupe conduisent généralement à l'existence d'une taille de groupe intermédiaire pour laquelle la survie et la reproduction des membres du groupe sont maximisées : c'est la taille de groupe optimale (Sibly 1983, Giraldeau and Gillis 1985). Cependant, cette taille de groupe pourrait ne jamais être observée. En effet, les groupes de taille optimale sont attractifs pour les individus immigrants qui cherchent à maximiser leur survie et leur reproduction. Ces individus, en s'ajoutant au groupe, vont augmenter la taille de ce dernier au-delà de la taille optimale, et donc induire une baisse de la survie et/ou de la reproduction des autres membres du groupe. On s'attend donc à ce que ces tailles de groupes soient instables et généralement plus grandes que l'optimale (Sibly 1983).

L'effet de la taille de groupe sur les paramètres démographiques des individus a rarement été testé directement. En effet, la majorité des études qui s'y sont intéressées se sont focalisées sur des espèces dont la reproduction est communautaire ou coopérative chez lesquelles le nombre d'*helpers* peut avoir un effet plus important sur la performance démographique des individus que le nombre total d'individus dans le groupe (Brown et al. 2003, Brouwer et al. 2006, 2020, Canestrari et al. 2008, Creel and Creel 2015, Guindre-Parker and Rubenstein 2020). De plus, certaines des études explorant le lien entre taille de groupe et paramètres démographiques ne donnent aucune information sur la pression de prédation dans le milieu, ou ont été conduites sur des sites où les prédateurs sont absents, dans lesquels les regroupements des proies ne découlent pas nécessairement d'une stratégie anti-prédateur (Waterman 2002, Altmann and Alberts 2003, Savage et al. 2009, Gager et al. 2016, Pillay and Rymer 2017). Enfin, la plupart des études explorant ce lien ont été conduites chez des espèces vivant dans des groupes instables où la taille des groupes ne reflète probablement pas des effets à long terme sur la performance démographique des individus, du fait de leur variabilité (Cheney and Seyfarth 1987, Brown and Brown 2004, Serrano et al. 2005, Watson et al. 2007, Brown et al. 2016).

De plus, quand une relation entre taille de groupe et démographie a été étudiée, la direction de la relation est très variable en fonction des études et des espèces : chez les mammifères, la survie des individus a été documentée comme étant positivement (Cheney and Seyfarth 1987, Rasa 1989, Rood 1990, Clutton-Brock et al. 1999), négativement (van Noordwijk and van Schaik 1999, Waterman 2002, Creel and Creel 2015) ou non corrélée (Waterman 2002, McGuire et al. 2002, Majolo et al. 2008, Savage et al. 2009, Gager et al. 2016) à la taille de groupe.

Les résultats des études portant sur le lien entre taille de groupe et succès reproducteur sont aussi mixtes puisque des études conduites sur différentes espèces ont montré que cette relation était soit positive (Robinson 1988, Canestrari et al. 2008, Watts and Holekamp 2009, Creel and Creel 2015), négative (Waterman 2002, Altmann and Alberts 2003, Ebensperger et al. 2011), non linéaire (Avilés and Tufiño 1998, Armitage and Schwartz 2000) ou absente (Mann et al. 2000, Pillay and Rymer 2017, Solomon and Keane 2018).

Chez les espèces sociales, la taille des groupes peut donc avoir d'importants effets sur le comportement des individus, leurs paramètres démographiques et la dynamique sociale des groupes. Cependant, à ce jour, les résultats des études qui se sont intéressées à l'effet de la taille de groupe sur le comportement des individus sont hétérogènes et le lien entre le comportement et les paramètres démographiques des individus reste mal compris. De plus, l'effet de la taille de groupe sur la survie et la reproduction des individus a fait l'objet de nombreuses recherches mais les résultats sont hétérogènes et la plupart des recherches se sont focalisées sur des espèces à reproduction communautaire ou coopérative. Enfin, l'effet de la taille de groupe sur la dynamique sociale est peu documenté, bien que les dynamiques des populations d'espèces sociales ne puissent être entièrement comprises sans prendre en compte les interactions entre les différents groupes sociaux constituant la population.

QUESTIONS ET PLAN DE THESE

Dans cette thèse, j'explore les effets de la taille de groupe sur le comportement, la démographie et la dynamique sociale d'un grand herbivore, le zèbre des plaines *Equus quagga*. Pour ce faire, j'utilise les données issues de deux populations sauvages, collectées dans le Parc National de Hwange (HNP) au Zimbabwe et dans le Parc de Hluhluwe-iMfolozi (HiP) en Afrique du Sud, qui sont deux sites où le risque de prédation pour les zèbres est élevé.

Le zèbre des plaines est un modèle d'étude idéal pour ces recherches pour plusieurs raisons : (i) les zèbres des plaines sont des animaux sociaux qui vivent dans des harems (groupes familiaux composés d'un mâle, d'une ou plusieurs femelles adultes, de subadultes des deux sexes et de jeunes dépendants de leur mère) dont la taille et la composition sont stables au cours du temps, (ii) la reproduction des zèbres n'est ni communautaire, ni coopérative, (iii) leurs patrons de rayures uniques permettent de suivre sur le long terme chaque individu de manière non invasive et d'estimer leur survie et leur succès reproducteur sans avoir besoin de marquer les animaux, (iv) les mâles célibataires se retrouvent dans des groupes de *bachelors* et tentent parfois de prendre possession d'un harem ce qui peut conduire à des changements d'étalon et potentiellement à des

comportements d'infanticide, et (v) les zèbres des plaines vivent dans des sociétés multi-niveaux où l'agrégation temporaire de plusieurs groupes sociaux (harems et/ou groupes de *bachelors*) est fréquente.

Dans le chapitre 1 intitulé « *Plains zebras bring evidence that dilution and detection effects may not always matter behaviorally and demographically* », j'explore l'effet de la taille de groupe sur l'un des paramètres démographiques des individus, et les mécanismes sous-jacents impliqués. En effet, peu d'études ont été capables de tester le lien direct entre la taille de groupe et la survie des individus chez les espèces dont la reproduction n'est ni communautaire, ni coopérative, et le lien entre les effets de dilution et de détection et la survie des individus en contexte de prédation reste essentiellement théorique. Pour ce faire, j'utilise des données comportementales et démographiques collectées dans la population de zèbre des plaines de HNP pour tester l'effet de la taille de groupe sur la vigilance anti-prédateur (individuelle et collective), l'acquisition des ressources, les interactions agonistiques et la survie des poulains et des adultes afin de répondre aux questions suivantes :

- La vigilance individuelle diminue-t-elle lorsque la taille de groupe augmente ?
- La vigilance collective augmente-t-elle lorsque la taille de groupe augmente ?
- L'acquisition des ressources augmente-t-elle lorsque la taille de groupe augmente ?
- La fréquence des interactions agonistiques entre individus d'un même groupe augmente-t-elle lorsque la taille de groupe augmente ?
- Le taux de survie des individus est-il positivement corrélé à la taille des harems ?

Dans le chapitre 2 intitulé « *Do infanticides occur in harem-forming equids? A test with long-term socio-demographic data in wild plains zebras* », j'explore l'effet de la taille de groupe, et plus particulièrement l'effet du nombre de femelles reproductrices dans les harems sur la fréquence des changements d'étalon dans ces harems, un effet montré chez quelques espèces mais encore jamais testé chez les équidés. L'effet de ces changements d'étalon sur la survie des poulains est aussi exploré afin de mettre en évidence ou non l'existence des comportements d'infanticides par les mâles chez le zèbre des plaines en milieu sauvage. En effet, chez les équidés, plusieurs études ont reporté des infanticides à la suite de changements d'étalon, mais la majorité de ces études ont été conduites sur des populations captives ou réintroduites. Chez les équidés sauvages, l'existence de ce comportement et son impact potentiel sur la dynamique des populations reste donc à démontrer. Pour ce faire, j'utilise des données démographiques et des données hormonales collectées dans la population de zèbre des plaines de HNP. Les données hormonales permettent de déterminer le statut de gestation des femelles et d'avoir connaissance

de la naissance de poulains qui auraient pu ne jamais être observés sur le terrain. Dans ce chapitre, l'objectif est de répondre aux questions suivantes :

- Les changements d'étalon au sein des harems sont-ils plus fréquents dans les grands harems comprenant davantage de femelles reproductrices que dans les petits harems ?
- La survie des poulains diminue-t-elle lorsqu'un nouvel étalon s'est établi dans le harem peu de temps avant ou après leur naissance (infanticide) ?

Dans le chapitre 3 intitulé « *Vegetation cover facilitates the avoidance of bachelors by larger harems in plains zebras, with consequences for stallion turnovers* », j'explore l'effet de la taille de groupe sur la dynamique sociale des zèbres. Plus particulièrement, j'étudie l'effet du nombre de femelles reproductrices dans les harems sur la probabilité de ces derniers à s'associer avec d'autres groupes (harems et/ou groupes de *bachelors*). En effet, les zèbres des plaines forment fréquemment des troupes ce qui peut avoir d'importants effets sur la dynamique de leurs populations, mais l'effet de la taille de groupe sur la dynamique de formation des troupes reste peu documenté. Pour ce faire, j'utilise des données démographiques collectées dans les populations de zèbre des plaines de HNP et HiP. Dans ce chapitre, je teste aussi l'effet du nombre de femelles reproductrices sur la fréquence des changements d'étalon dans les harems dans la population de HiP, de manière similaire à l'analyse qui a été conduite dans le chapitre 2 pour la population de HNP. Dans ce chapitre, je cherche à répondre aux questions suivantes :

- Les grands harems comprenant un grand nombre de femelles reproductrices, qui devraient bénéficier d'une meilleure protection contre les prédateurs, sont-ils plus souvent observés seuls que les petits harems ?
- Les grands harems comprenant un grand nombre de femelles reproductrices, qui devraient être davantage exposés à des risques de harcèlement des femelles par les *bachelors* et à des risques de changement d'étalon, s'associent-ils plus avec d'autres harems et moins avec les groupes de *bachelors* que les petits harems ?

Enfin, dans l'analyse complémentaire et préliminaire intitulé « *Herd formations between pairs of harems in the multilevel society of plains zebra: how long do they last, and how often, when and where do they occur?* », j'utilise des données GPS collectées dans la population de HNP pour documenter la fréquence, la durée et la distribution temporelle et spatiale des formations de troupes (événements de fusion) entre dyades (paires de harems), puisque cela a été peu documenté jusqu'à présent. Dans cette analyse, je tente de répondre aux questions suivantes :

- Combien de temps les dyades restent-elles ensemble ?

- La fréquence des associations entre dyades et la proportion de temps que ces dernières passent ensemble sont-elles liées au chevauchement de leurs domaines vitaux ?
- Les dyades voyagent-elles sur de longues distances ensemble ?
- Restent-elles à proximité de leur point de rencontre ?
- Lorsque l'eau se fait rare, les localisations où les dyades sont ensemble sont-elles enregistrées davantage à proximité des points d'eau que les localisations où les dyades ne sont pas ensemble ?
- Les dyades s'associent-elles davantage pendant les périodes où le risque de prédation est élevé (c.-à-d. la nuit, à l'aube et au crépuscule) ?

MATERIEL ET METHODES



MODELE D'ETUDE

Les équidés font partie de l'ordre des Périssodactyles qui comprend trois familles : les Equidés, les Rhinocérotydés et les Tapiridés. Le zèbre des plaines fait partie des sept espèces d'équidés sauvages actuellement présentes dans le monde, comprenant trois espèces de zèbres que sont le zèbre des plaines, le zèbre de Grevy *Equus grevyi* et le zèbre des montagnes *Equus zebra*, trois espèces d'ânes sauvages que sont l'âne sauvage d'Afrique *Equus africanus*, l'âne sauvage d'Asie *Equus hemionus* et le kiang *Equus kiang*, et une espèce de cheval sauvage, le cheval de Przewalski *Equus ferus przewalskii*. Bien qu'elle soit l'espèce la plus abondante de tous les équidés sauvages et celle avec l'aire de distribution la plus large (Hack et al. 2002, Ransom and Kaczensky 2016) (Fig. 1), la population globale de zèbre des plaines tend à décliner. Entre 2002 et 2016, elle a été réduite par 24% et en conséquence l'espèce, qui était classée dans la catégorie « préoccupation mineure » (LC) sur la Liste rouge de l'IUCN en 2002, se retrouve désormais classée dans la catégorie « quasi menacée » (NT) (King and Moehlman 2016) et est proche d'être classée dans la catégorie « vulnérable » (VU).

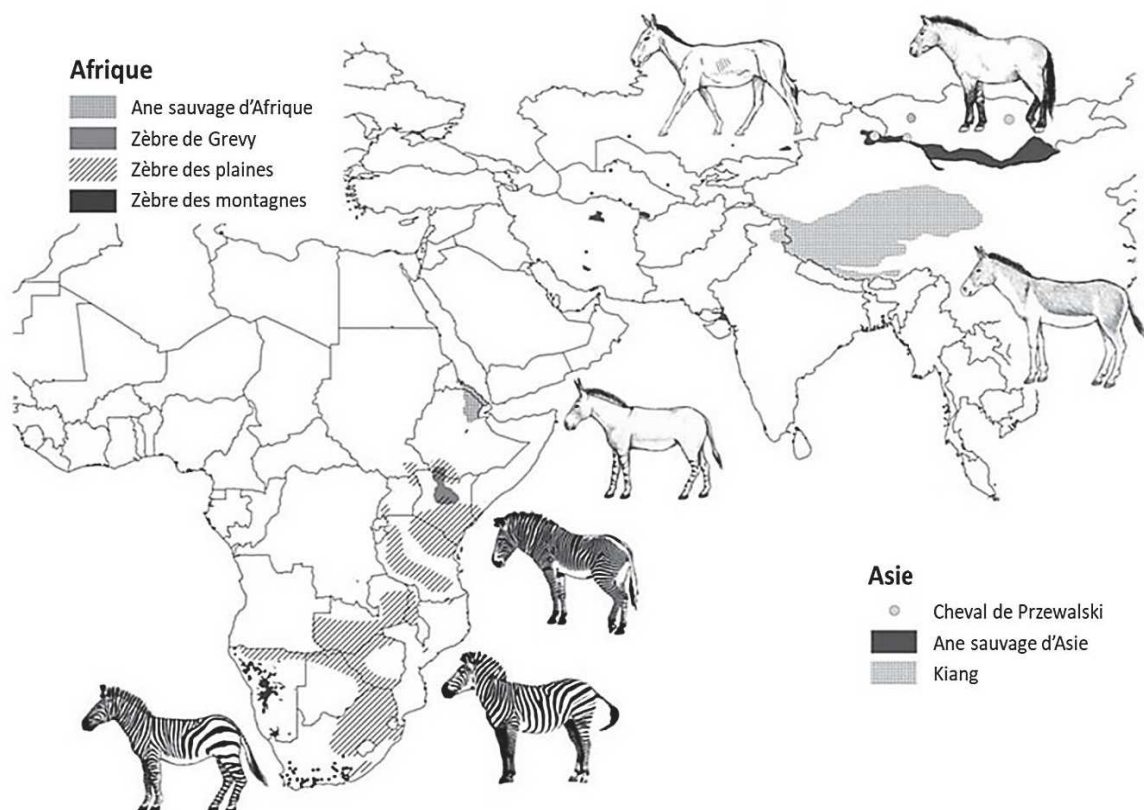


Figure 1. Distribution actuelle des équidés sauvages dans le monde (image extraite et adaptée de Ransom and Kaczensky 2016)

Les équidés sauvages sont des animaux sociaux et leur organisation sociale est classifiée en deux types distincts (Klingel 1974, 1975, Rubenstein 1986). Le type I inclut les espèces formant des

harems chez lesquelles les mâles peuvent contraindre les femelles et les défendre contre d'autres mâles. C'est le cas du zèbre des plaines, du zèbre des montagnes et du cheval de Przewalski. Les chevaux féroces *Equus ferus* et les ânes féroces *Equus asinus* présentent aussi ce type d'organisation sociale. Le type II est composé des espèces territoriales chez lesquelles les mâles contrôlent indirectement les femelles en défendant des territoires ou des ressources contre les autres mâles. On retrouve ce type d'organisation chez le zèbre de Grevy, l'âne sauvage d'Afrique, l'âne sauvage d'Asie et le kiang.

Les populations de zèbre des plaines sont constituées de deux unités sociales de base : les harems et les groupes de *bachelors* (Klingel 1969b, Estes and Otte 2012). Les harems sont composés d'un étalon (mâle du harem) et la plupart du temps de plusieurs femelles adultes, de subadultes des deux sexes, et de jeunes dépendants de leur mère. La taille moyenne des harems varie entre 4.5 et 7.1 individus dans diverses populations, le nombre maximum d'individus par harem atteignant parfois jusqu'à 16 individus (Klingel 1969b). Les mâles qui ne sont pas établis dans des harems forment des groupes de *bachelors* (mâles célibataires) dont la taille et la composition sont très variables au cours du temps. La taille moyenne des groupes de *bachelors* varie entre 1.6 et 3 individus dans plusieurs populations, le nombre maximum d'individus atteignant parfois jusqu'à 40 individus (Klingel 1969b, Rubenstein and Hack 2004). Les jeunes dispersent vers l'âge de 2 ans : les jeunes femelles rejoignent un harem déjà existant ou forment un nouveau harem avec un *bachelor*, et les jeunes mâles rejoignent des groupes de *bachelors*. Les femelles subadultes et adultes peuvent aussi changer de groupe mais ces événements sont rares : 92% (N = 453) et 95% (N = 290) des femelles sont toujours dans le même harem après un an, et 86% (N = 342) et 97% (N = 76) après deux ans, dans les populations de HNP et HiP respectivement. Les harems et les groupes de *bachelors* se rejoignent fréquemment et forment alors des troupes, définissant des sociétés multi-niveaux. Dans ces dernières, les groupes sociaux se rassemblent de manière temporaire puis se séparent en leurs unités sociales de base (Grueter et al. 2012), à la différence d'autres formes de systèmes de fission-fusion où les groupes qui s'agrègent se séparent ensuite en sous-groupes qui varient en termes de taille, de composition et de degré de cohésion (Grueter et al. 2012). Ces formations de troupes varient en taille (comprenant parfois jusqu'à plusieurs centaines d'individus) et en composition (comprenant des harems et des groupes de *bachelors*, ou seulement des harems) (Rubenstein and Hack 2004).

Les zèbres des plaines sont principalement brouteurs et sont donc majoritairement associés aux zones ouvertes telles que les prairies. Les zèbres adultes sont dépendants d'un apport régulier en eau et restent le plus souvent à proximité des points d'eau (Bell 1971, Estes and Otte 2012). Leur système digestif monogastrique, différent de celui des ruminants, leur permet d'extraire de l'énergie à partir de fourrages de basse qualité et de survivre dans des conditions où les ruminants ne pourraient subvenir à leurs besoins énergétiques (Duncan 1992). Les zèbres se nourrissent essentiellement d'herbes, tout comme le gnou bleu *Connochaetes taurinus*, le buffle d'Afrique *Syncerus caffer* et le cobe à croissant *Kobus ellipsiprymnus*, trois espèces de bovidés qui coexistent avec les zèbres dans de nombreux parcs africains et qui peuvent potentiellement entrer en compétition avec les zèbres pour l'accès aux ressources alimentaires (bien que cela dépende d'autres facteurs tels que la saison, l'abondance de chaque espèce, ou la hauteur de la végétation).

Les recherches conduites sur les zèbres des plaines se sont initialement focalisées sur leur organisation sociale (Klingel 1969b, Penzhorn 1984, Rubenstein 1986) et leur reproduction (Klingel 1969a, Smuts 1976b). Le comportement des zèbres des plaines a été documenté en 1974 par Klingel et de nombreux travaux de recherche sur ce sujet ont suivi : des études se sont par exemple intéressées au budget d'activité (Neuhaus and Ruckstuhl 2002), au leadership (Fischhoff et al. 2007a), à la sélection de l'habitat (Fischhoff et al. 2007b, Courbin et al. 2016, 2019, Makin et al. 2017, Patin 2018, Mandinyanya et al. 2020), aux comportements d'infanticide par les mâles (Pluháček and Bartoš 2000, 2005, Pluháček et al. 2006, Ransom and Kaczensky 2016), à la vigilance (Simpson et al. 2012, Schmitt et al. 2014, 2016, Creel et al. 2014, Barnier et al. 2016, Makin et al. 2017, Périquet et al. 2017) et à l'acquisition des ressources (Barnier et al. 2014, Creel et al. 2014, Périquet et al. 2017). Cependant, l'effet de la taille de groupe sur le comportement des zèbres des plaines a rarement été investigué (Schmitt et al. 2014, Périquet et al. 2017, Patin 2018) et les résultats produits sont mixtes : l'étude de Schmitt et al. (2014) a démontré une corrélation négative entre vigilance individuelle et taille de groupe, alors qu'une absence de relation a été trouvée par Périquet et al. (2017). Quelques études ont également exploré les paramètres démographiques et identifié les facteurs régulant ou limitant les populations de zèbre des plaines (Smuts 1976a, Georgiadis et al. 2003, Grange et al. 2004, 2015, de Vos et al. 2020). Cependant, l'effet de la taille de groupe sur les paramètres démographiques des populations et le lien entre ces paramètres et le comportement des zèbres des plaines n'ont jamais été étudiés. La dynamique sociale des zèbres des plaines a aussi fait l'objet de quelques études (Rubenstein and Hack 2004, Fischhoff et al. 2009) mais l'effet de la taille de groupe sur cette dynamique sociale reste mal connu.

SITES D'ETUDES

Les données utilisées dans le cadre de cette thèse ont été collectées dans deux sites d'études : le Parc National de Hwange au Zimbabwe et le Parc de Hluhluwe-iMfolozi en Afrique du Sud (Fig. 2).

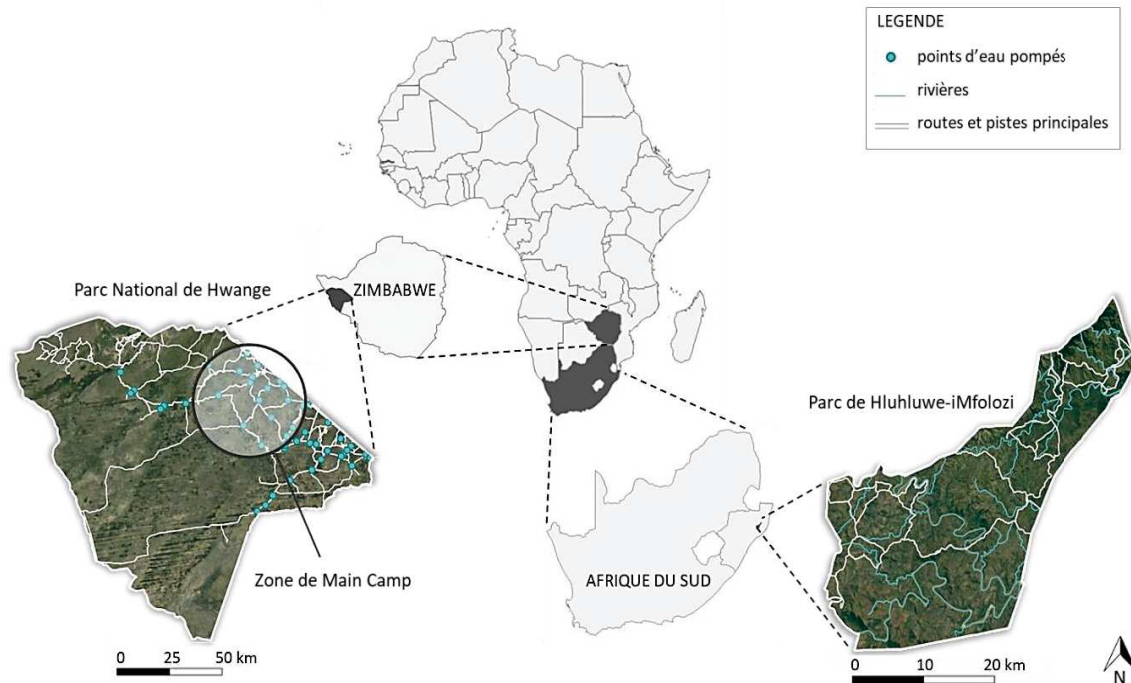


Figure 2. Localisation du Parc National de Hwange (superficie : 15 000 km²) à l'Ouest du Zimbabwe et du Parc de Hluhluwe-iMfolozi (superficie : 900 km²) situé dans la province du KwaZulu-Natal à l'Est de l'Afrique du Sud.

Le Parc National de Hwange (HNP) se situe dans le Nord-Ouest du Zimbabwe (19°00'S, 26°30'E) (Fig. 2). Le parc est principalement couvert de forêts et de buissons, entrecoupés par des zones de prairies ouvertes situées autour des points d'eau ou en fond de vallée (Rogers 1993, Chamaille-Jammes et al. 2006). La végétation majoritairement composée de *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* et *Terminalia sericea* est caractéristique d'une savane dystrophique semi-aride (Rogers 1993). La saison des pluies dure de Novembre à Avril et la saison sèche de Mai à Octobre. Le taux de précipitation annuel est en moyenne de 600 mm, la majorité des pluies tombant entre Novembre et Avril (Chamaille-Jammes et al. 2006) lors de la saison des pluies. A cause de cette forte saisonnalité, la disponibilité en eau est très variable : en saison des pluies, l'eau est disponible dans tout le parc, mais en saison sèche, elle n'est disponible qu'à un nombre limité de points d'eau pompés (Fig. 3). Ces points d'eau permettent aux espèces dépendantes d'un apport régulier en eau, telles que le zèbre des plaines, d'avoir accès à cette ressource tout au long de l'année. Ils aident également au maintien d'une forte densité d'espèces animales dans le parc durant la saison sèche. A HNP, la densité des zèbres

est estimée aux environs de 1 individu par km² de 2004 à aujourd'hui (Chamaillé-Jammes et al. 2009, Grange et al. 2015, données non publiées). Les zèbres des plaines y coexistent avec une large guildes de prédateurs, connus pour attaquer à la fois de jeunes zèbres et des zèbres adultes : la densité de lion, leur principal prédateur, fluctue à HNP autour de 3.5 lions pour 100 km² (Loveridge et al. 2016), et d'autres prédateurs tels que le léopard *Panthera pardus*, la hyène tachetée *Crocuta crocuta* et le guépard *Acinonyx jubatus* sont également présents mais en plus faible densité. Les zèbres sont l'une des proies favorites des lions à HNP, représentant 7.1% des proies tuées par les lions, derrière les buffles d'Afrique, les éléphants d'Afrique *Loxodonta africana*, les gnous bleus et les girafes *Giraffa camelopardalis* (Loveridge et al. 2006).



Figure 3. Photographies de l'un des points d'eau pompés du Parc National de Hwange (point d'eau *Makwa*) en saison des pluies et en saison sèche.

Le Parc de Hluhluwe-iMfolozi (HiP) est situé dans l'Est de l'Afrique du Sud, dans la province du KwaZulu-Natal (28°00'-28°26'S, 31°43'-32°09'E) (Fig. 2). La section nord du parc, Hluhluwe, et la section sud du parc, iMfolozi, sont d'une superficie d'environ 300 km² et 600 km², respectivement (Fig. 2). La végétation dans le parc est variée, allant des forêts fermées aux prairies (Howison et al. 2017). A Hluhluwe, quatre espèces majoritaires composent les forêts : *Acacia nilotica*, *Euclea divinorum*, *Celtis africana* et *Acacia karoo*. A iMfolozi, les forêts sont composées essentiellement de trois espèces : *Acacia nigrescens*, *Acacia tortilis* et *Spirostachys africanus* (Whateley and Porter 1983). L'altitude et le taux de précipitation varient au sein du parc, diminuant de Hluhluwe (990 mm par an et 750 m d'altitude) vers iMfolozi (635 mm par an et 60 m d'altitude). La plupart des précipitations tombe pendant la saison des pluies, qui dure d'Octobre à Mars (Howison et al. 2017). La rivière *Hluhluwe* au nord et les rivières *Black* et *White* au sud sont les trois principales rivières pérennes du parc. De nombreux points d'eau temporaires sont également présents dans tout le parc à la saison des pluies. Le parc est pratiquement dépourvu de sources d'eau artificielles. La population de zèbres des plaines à HiP est estimée aux environs de 2 individus par km² de 2010 à aujourd'hui (Le Roux et al. 2017, données non

publiées). Toute une guildes de prédateurs est présente dans le parc, incluant lions, léopards, hyène tachetées et guépards.

Depuis Juillet 2004 à HNP et Novembre 2017 à HiP, un suivi démographique des populations de zèbres des plaines sur ces deux sites d'études a été mis en place. Ce suivi est conduit sur la totalité du parc à HiP (suivi de l'ensemble des individus), contrairement à HNP où seuls les individus de la zone de *Main Camp* (d'une superficie d'environ 2000 km²; Fig. 2) sont suivis. Deux fois par an, une fois en saison des pluies (entre Novembre et Avril) et une fois en saison sèche (entre Mai et Octobre), les groupes de zèbres composés d'individus connus sont recherchés. Lorsqu'un groupe est trouvé, la taille du groupe et sa composition sont notées. La taille des harems varie de 2 à 10 individus (moyenne = 5, médiane = 5) à HNP entre 2008 et 2017, et de 2 à 13 individus (moyenne = 5, médiane = 5) à HiP entre 2017 et 2020 (Fig. 4A). La taille des groupes de *bachelors* varie de 1 à 19 individus (moyenne = 4.5, médiane = 3) à HNP entre 2018 et 2019, et de 1 à 9 individus (moyenne = 3.6, médiane = 3.5) à HiP entre 2017 et 2020 (Fig. 4B). L'âge des individus observés pour la première fois est estimé à l'aide du critère de Penzhorn (Penzhorn 1982) combiné avec des photos de poulains d'âge connu, et le comportement d'allaitement est utilisé pour déterminer la maternité (Barnier et al. 2012). Plus de détails sur ce suivi démographique peuvent être trouvés dans Grange et al. (2015). En parallèle, des échantillons de crottins de femelles sont collectés de manière opportuniste (à HNP seulement) : l'analyse de la concentration en hormones de ces échantillons permet de déterminer le statut de gestation des femelles (Ncube et al. 2011). Egalement, 34 femelles adultes de différents harems ont été équipées de colliers GPS entre 2009 et 2017 à HNP, permettant ainsi d'obtenir des données sur le déplacement des harems.

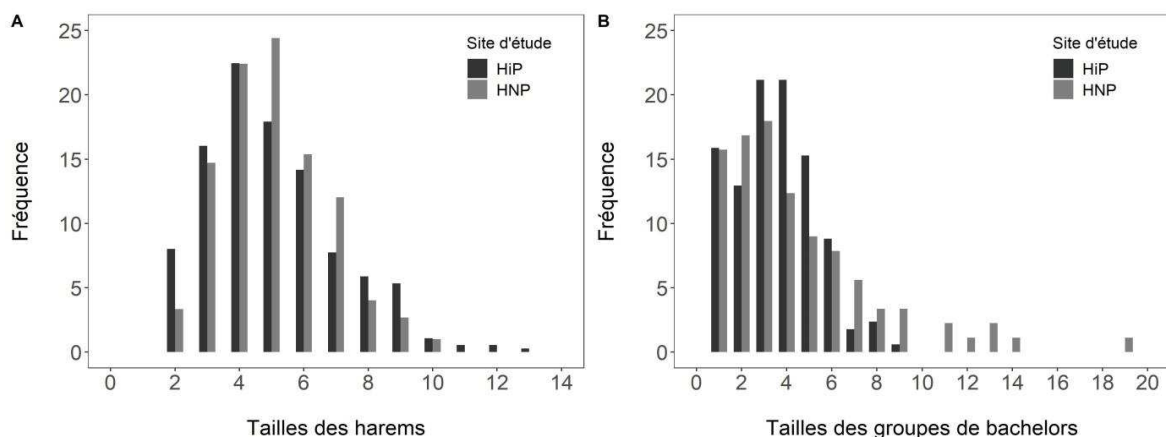


Figure 4. Distribution des tailles des harems (A) et des groupes de *bachelors* (B) observés dans le Parc de Hluhluwe-iMfolozi (HiP) et le Parc National de Hwange (HNP). Les fréquences sont standardisées au nombre total de harems et de groupes de *bachelors* observés dans chacun des deux sites d'études.

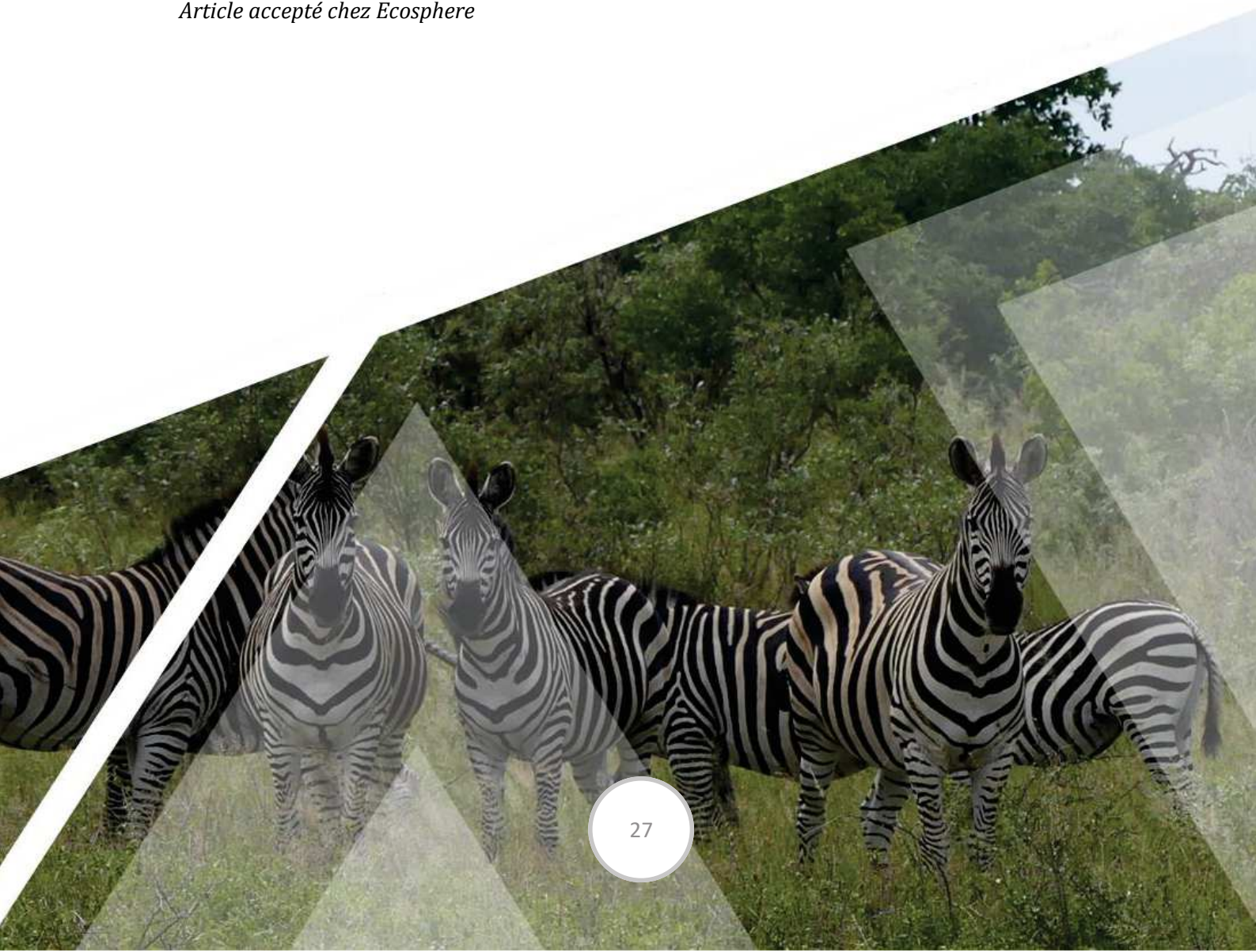
CHAPITRE 1

Plains zebras bring evidence that dilution and detection effects may not always matter behaviorally and demographically

Les zèbres des plaines apportent la preuve que les effets de dilution et de détection pourraient ne pas toujours avoir d'importance sur le plan comportemental et démographique

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ABSTRACT

Group living is assumed to benefit prey by reducing predation risk due to dilution and detection effects. This increased safety could be exchanged against a reduced individual vigilance leading to increased foraging and fitness until costs of intra-group competition offset this benefit. However, very few studies have been able to directly test the relationship between individual fitness and group size in non-cooperative breeding species. Therefore, evidence that dilution and detection effects do indeed translate into increased fitness under predation risk remains mostly theoretical. Here we aimed at empirically testing whether group size influences beneficial and costly behaviors, and ultimately the survival of individuals, in a prey species facing heavy predation pressure. We focused on plains zebra *Equus quagga* of Hwange National Park in Zimbabwe, a high lion density area. We collected behavioral data (i.e. individual vigilance and foraging, collective vigilance, and agonistic interactions) that we used as proxies to investigate the costs and benefits of grouping in this species. We then fitted multistate capture-mark-recapture and Cox proportional-hazards models to estimate apparent survival of adults and young zebras respectively, and assess whether a demographic signal of group size could be found. Our results show that collective vigilance increases with group size, a prerequisite of the detection effect, but individual vigilance does not consistently decrease with group size, which suggests that there is no group size effect on individual vigilance. Agonistic interactions were rare. These results suggest that there are no foraging costs of grouping here, and even some benefits such as a better collective vigilance. However, any benefits of being in larger groups did not translate into increased survival, as we found no effect of group size on the apparent survival of individuals. Since dilution and detection effects do not matter behaviorally and demographically in these plains zebras living under high predation risk, these results challenge our understanding of how predation shapes animal sociality: fitness benefits of dilution or detection should not be assumed.

KEYWORDS: demography, grouping behavior, predation risk, sociality, ungulate

INTRODUCTION

Grouping strategies vary between- and within species, ranging from solitary life, fusion-fission systems where group size changes regularly, to stable groups (Clutton-Brock 2016, Ward and Webster 2016). It is assumed that this diversity was favored by natural selection on individuals, and that group sizes reflect the trade-offs between benefits and costs of grouping (Krause and Ruxton 2002). In prey species, one of the main assumed benefits of living in groups is reduced predation risk. Two, non-mutually exclusive, reasons are usually brought forward. First, as group size increases, the presence of additional group members could dilute the risk for each individual of being predated during an attack, under the assumption that the predator can only take one prey at a time and that attack rate does not increase with prey group sizes (the dilution effect ; Bertram 1978, Turner and Pitcher 1986, Lehtonen and Jaatinen 2016). Second, with increasing group size, the probability of detecting an approaching predator could increase as more individuals monitor the environment (the detection effect; Lima 1995, Pulliam 1973). Several studies have given support to these two effects (see Beauchamp 2015 chapters 2 & 5 for a review). Increased safety in larger groups may allow individual to reduce their vigilance level, leading to increased foraging (the so-called group size effect on vigilance; Beauchamp 2008, Elgar 1989, Lima 1995, Roberts 1996). However, living in groups also incurs costs such as increased intra-group competition for resources, due to either interference between group members or depletion of resources (Amano et al. 2006, Blanchard et al. 2008).

These assumed costs and benefits of group living have been widely studied, but with mixed conclusions. For instance, the reduction of individual vigilance with group size, likely leading to increased foraging, has often been observed (Elgar 1989, Lima and Dill 1990). Studies failing to detect such relationship are also common however (Treves 2000, Beauchamp 2008), which could potentially be explained by the existence of alternative antipredator strategies other than vigilance such as grouping (Creel et al. 2014) and adjusting space use in response to predation risk (Creel et al. 2005, Patin et al. 2019). Mixed results have also been obtained when directly investigating the relationship between group size and foraging rates. In the specific case of ungulates, this relationship has been found to be either positive (Isvaran 2007, Barnier et al. 2016), negative (Molvar and Bowyer 1994, Focardi and Pecchioli 2005) or absent (Périquet et al. 2017). Similarly, in ungulates, frequency of agonistic interactions between group members was found to be either positively (Molvar and Bowyer 1994), negatively (Risenhoover and Bailey 1985) or not correlated to group size (Fortin et al. 2004).

If costs and benefits of group living exist and are significant, these ultimately affect the fitness of individuals. As costs and benefits of group living should vary between species and environments, it is unclear what shape the relationship between group size and fitness should take in specific cases (Sibly 1983, Krause and Ruxton 2002). Generally, fitness is expected to increase with group size up to an optimal size, when the costs of increased intra-group competition offset these benefits at larger group sizes (Sibly 1983, Markham et al. 2015). Few studies have tested the relationship between group size and individual fitness under predation risk directly. There are several explanations for this. First, most empirical studies come mainly from research focused on species that do not live in stable groups, for which group size is unlikely to translate into long-term effects on fitness as it often fluctuates (Cheney and Seyfarth 1987, Brown and Brown 2004, Serrano et al. 2005, Watson et al. 2007, Brown et al. 2016). Second, some of these studies do not provide information on predation pressure or are conducted in predator-free environments in which grouping behavior of prey species might not necessarily reflect an antipredator strategy (Waterman 2002, Altmann and Alberts 2003, Savage et al. 2009, Gager et al. 2016, Pillay and Rymer 2017). Finally, numerous studies focus on cooperative breeding species for which the effect of the number of helpers is more likely to affect individual fitness than the number of individuals in the group (Brown et al. 2003, Brouwer et al. 2006, 2020, Canestrari et al. 2008, Creel and Creel 2015, Guindre-Parker and Rubenstein 2020).

It is also noteworthy that empirical results on the relationship between group size and survival, a key component of fitness, are inconsistent. In mammals for instance, juvenile survival has been found to be positively (Cheney and Seyfarth 1987, Rasa 1989), negatively (van Noordwijk and van Schaik 1999, Waterman 2002) or not correlated (Majolo et al. 2008, Savage et al. 2009) with group size. Similarly, adult survival has been found to be positively (Rood 1990, Clutton-Brock et al. 1999), negatively (Creel & Creel, 2015) or not correlated (Waterman 2002, McGuire et al. 2002, Gager et al. 2016) with group size. Taken together, these studies therefore suggest that the existence of dilution and detection effects that would have large effects on survival should not be taken for granted.

Here, we tested whether group size affects foraging and vigilance, and ultimately the survival of individuals in a prey population facing heavy predation pressure. We did so by studying a gregarious species, plains zebra *Equus quagga*, in Hwange National Park (HNP) in Zimbabwe, a system characterized by a high predator pressure (Loveridge et al. 2016). We first tested whether individuals adjust their behavior (i.e. individual vigilance and foraging, collective vigilance, and agonistic interactions) with group size. This would offer a basis to explain any relationship

between group size and survival, which we also investigated (see below). With increasing group size, we expected (1) reduced individual vigilance, (2) increases in time spent foraging, and (3) increased collective vigilance, defined as having at least one individual vigilant (Lima 1995). However, as we also expected increased levels of agonistic interactions between group members in larger groups, we expected that these predictions might not be valid for the largest groups. We then investigated whether harem size affects the survival of individuals, using long-term individual-based monitoring data. We used Cox proportional-hazards and multistate capture-mark-recapture (CMR) models to assess the effect of group size on apparent survival of foals and adults. Since individuals in smaller groups are expected to experience greater predation, we predicted increased survival probabilities of both age-classes with increasing group size, but only up to a point, where increased intra-group competition might induce costs of being in larger groups. Overall, by combining behavioral observations and long-term demographic data, we offer a rare opportunity for a comprehensive test of the demographic consequences of dilution and detection effects under a high level of predation.

MATERIAL AND METHODS

Study site and species

The study was conducted in the eastern section of HNP in western Zimbabwe over an area covering c. 2000 km² (19°00'S, 26°30'E). The vegetation is dominantly bushy but interspersed with patches of open grasslands. The annual rainfall averages 600 mm, with most rain falling between November and April. In the hot dry season (September-October), water is only available in a limited number of pans where groundwater is pumped. In the study area, these pans allow water-dependent species to have access to water year-around.

We used plains zebra as model species. In HNP, plains zebra density varies around 1 individual km⁻² (Chamaillé-Jammes et al. 2009b). Plains zebra populations are made of two basic social units: harem and bachelor groups (Klingel 1969b). Non-territorial, the harems are composed of a stallion (i.e. harem-male) and most often several adult females (unrelated, as female disperse from natal groups when they are around 2 years old (y.o.)), subadults of both sexes, and dependent offspring. In the study area, harem sizes (without foals) range between 2 and 9 individuals (Fig. 1). Non-harem males form all-male bachelor groups, of 1-19 individuals (median: 3 individuals). All individuals used in this study were identified, using the stripes patterns that are unique to each individual, in the context of an ongoing long-term demographic study. We categorized individuals across four age-classes: foal, from birth to 1 y.o.; yearling, between 1 and

2 y.o.; subadult, between 2 and 4 y.o.; and adults, 4 y.o. and older. Young males and females disperse when they are around 2 y.o.: natively dispersing females join existing harems and males join bachelor groups. For reasons linked to sample size, in subsequent analyses subadults and adults were grouped in the same age-class termed 'adult'.

Harems and/or bachelor groups regularly aggregate with others in larger groups (referred to as 'herds' hereafter), defining a multi-layered social system (Klingel 1969b). Stability of herds is low, likely a few hours or less (pers. obs. and unpublished data from GPS collars). Stability of lower social layers, i.e. bachelor groups or harems, is greater. Some bachelors appear to spent months, if not years, together (unpublished data). Size and composition of bachelor groups had however not been consistently recorded during the historical demographic monitoring we based our analysis on, and we therefore focused our study on harems. Harem size is highly stable over time. A stallion is always present, and although subadult and adult females may change group, this is rare: in this study, after one year 92% of mares (n=453) and after two years 86% of mares (n=342) were still in the same harem. Therefore, we studied the relationship between behaviors and harem or herd size (as both harem size and herd size can be defined at the time t when behavior is observed), but studied the relationship between survival and harem size only (as, due to instability, herd size cannot be defined over the time interval over which survival is estimated, and an average herd size cannot be estimated unless near-continuous long-term observation is possible, which was not the case here).

Collection and analysis of behavioral data

We collected data on the behavior of zebras during 2 wet and 2 dry seasons (in 2018 and 2019). We conducted direct observations, videotaped for later analysis, during daytime using a car as a hide. We considered individuals to be part of the same group when the distance between them was below 50 m: in the field, this distance threshold (also used by Barnier et al. 2016) is adequate to separate isolated harems or groups that are in close contact from other groups of individuals located further away, and is thus relevant to study group-level dilution and detection effects. We focused on vigilance, foraging, and agonistic behaviors.

We studied individual vigilance and foraging using a focal-sampling approach (Altmann 1974). An individual was considered to be vigilant when it was stationary with the head raised above the shoulder and scanning the surroundings, and to be foraging when it was grazing. Based on the scanning direction of individuals, we focused on anti-predator vigilance and avoided conducting a focal observation if the animal was vigilant towards conspecifics. We studied only individuals in groups whose main activity was foraging to prevent movement or change in group

size or composition during focal samples. To obtain a large sample size within the limited time available, we only recorded, for each focal harem, data on the stallion and on one female, whose reproductive status (lactating or not) was recorded. A female was considered to be lactating if she had a foal (i.e. from birth to 1 y.o.). If a least one non-lactating and one lactating female were present in the group, we recorded data on one female of each status. As we conducted our research in the same study area during the whole study period, we could not avoid to occasionally repeating observations on the same individuals (number of focal per individual: min=1, max=11, median=1, mean=2.6). For each studied individual, we measured the duration of one bout of vigilance and the duration of the foraging bouts that immediately preceded and followed this vigilance bout. We only focused on active vigilance (i.e. head above shoulder), differentiating between free (i.e. while chewing) and costly vigilance (i.e. scanning exclusively). We recorded whether vigilance shifted from free to costly vigilance or whether foraging shifted to vigilance in response to a sudden external stimulus or to agonistic interactions (i.e. threat, push, chase or attack behaviors). This allowed us to (1) remove from the data the variability linked to external stimuli, by removing the affected bouts from the analyses (4 of the 992 bouts recorded), and (2) get an estimate of the proportion of foraging bouts interrupted by agonistic interactions, which partially reflects the strength of intragroup interference in the access to food resources. As costly vigilance bouts were rare (35 of the 352 bouts of vigilance recorded), we choose to analyze only focals during which the individual was in free vigilance. We collected data to control for the multiple factors that could influence antipredator vigilance and could either mask or reinforce the group size effect (Elgar 1989, Beauchamp 2015). We systematically recorded individual variables (i.e. age class, sex and reproductive status), type of group (i.e. 'harem' or 'herd', when the focal harem is isolated or surrounded by other zebra groups within 50 m, respectively), zebra group size (i.e. number of zebras in a 50-m radius, without considering foals but including any other zebras from the focal harem or from other harems or bachelor groups), number of foals in the group, and the presence of others prey species in a 50-m radius. We also estimated distance to cover as cover can provide ambush opportunities for lions. The distance between zebras and our vehicle (distance to observer) was also estimated, but these zebras are habituated to vehicles and tolerated vehicles at 5-50 m. As proxies for visibility, we recorded grass height ('short' when below focal zebra's hooves, 'tall' when above focal zebra's tibia, which is above the level of a zebra's eyes when feeding, and 'medium' when at intermediate height). We recorded wind strength using Beaufort number given by an anemometer ('none' (0 km h^{-1}), 'low' ($0 - 1.8 \text{ km h}^{-1}$), 'medium' ($1.8 - 7.4 \text{ km h}^{-1}$), and 'strong' ($> 13 \text{ km h}^{-1}$)) as zebras could be more vigilant in windy conditions that may affect the perception of predator cues. In total, we analyzed 282 focal observations (122 for males, 89 for non-lactating females and 71 for lactating females). In 2018,

we collected 138 and 35 focal samples in the wet and dry season respectively, and in 2019, we collected 49 and 60 focal samples in the wet and dry season respectively.

We tested the effect of group size on the duration of vigilance and foraging bouts by fitting generalized linear mixed-effects models using the R package *lme4* (Bates et al. 2015). We first built full models with the duration of vigilance or foraging bouts as response variable (we assumed Poisson-distributed errors), and the main and interactive effects of group size, season, and a variable coding for sex and reproductive status (male, lactating female, non-lactating female) as fixed effects. We also added a set of additive effects to control for the effects of variables which were not of interest here but were known to affect vigilance or foraging: presence/absence of other species, duration of the precedent foraging/vigilance bout, distance to cover, distance to observer, grass height and wind strength. We included the identity of the individual as random intercept to take into account individual differences in average bout duration. We also included observation-level random intercepts to correct for over-dispersion (Harrison 2014). These models were run separately for harem and herds, as the very high correlation between group size and group type prevented including them meaningfully in the same models. We also ran these models with a second-order polynomial effect of group size to allow the relationship between the response variable and group size to be non-linear, as expected by optimal group size models. From these full models, we conducted variable selection using the Akaike Information Criterion corrected for small sample sizes (AICc), considering only informative parameters (Arnold 2010), i.e. those reducing AICc by >2 . Variable selection was performed using the R package *MuMIn* (Bartoń 2009).

We studied the potential for collective vigilance using the scan-sampling approach (i.e. instantaneous sampling on groups) (Altmann 1974). We focused only on groups whose main activity was foraging. For each group studied, and every minute for 5 min, we performed a scan on the whole group and counted the number of individuals vigilant in the group (without considering foals which we assumed naïve regarding predation risk). We could thus compute the proportion of time (i.e. proportion of scans) when at least one individual in the group was vigilant, which is a metric of collective vigilance (Pays et al. 2007b, 2007c, 2012). We recorded the same control variables as for the study of individual vigilance and foraging (see above). As we conducted our research in the same study area during the whole study period, we could not avoid occasionally having repeated observations of the same groups (number of scan sequence per group: min=1, max=7, median=1, mean=1.7). In total, we analyzed 475 scan samples (95 scan sequences of 5 scans each). In 2018, we collected 35 and 15 scan sequences in the wet and dry

season respectively, and in 2019, we collected 23 and 22 scan sequences in the wet and dry season respectively.

For statistical inference on these ‘collective vigilance’ data, we used an approach similar to that used for the study of the duration of vigilance/foraging bouts. The response variable was the proportion of scans in an observation sequence where at least one individual was vigilant, and we assumed binomial distribution of errors. For harems, the fixed effects of the models were the same as for the study of the duration of vigilance/foraging bouts (except for sex and reproductive status of individuals and the duration of the precedent bout). Random effects were changed: the random intercept was for harem identity, and observation-level random effects were not required. For herds, there were no repeated observations of specific herds, as herd represented different group aggregation each time, and we therefore did not include random effects and fitted the models using the R package *stats* (R Core Team 2019). Since sample sizes were small for herds (20 scan sequences), the full model for herds only included the interactive effects of group size and season, as adding other control variables led to strong overfitting. We performed the same AICc-based variable selection as for the study of the duration of vigilance/foraging bouts.

We studied agonistic interactions using the all-occurrence sampling approach (Altmann 1974). Agonistic interactions during foraging were studied during the study of vigilance and foraging (see above). Additionally, we conducted 10-min observations of groups when individuals were resting, and 1-min observations of groups that were travelling. The 1-min duration was constrained by the fact that travelling groups often rapidly disappeared in the bushes. For both types of observation, we counted the number of agonistic interactions observed during the observations periods to estimate the frequency of agonistic interactions. In total, we analyzed 32 sequences of 10-min observations when zebras were resting, and 46 sequences of 1-min observations when they were travelling. As previously, we could not avoid repeating observations of same groups occasionally (number of observations group⁻¹ resting: min=1, max=4, median=1, mean=1.3; number of observations group⁻¹ travelling: min=1, max=12, median=1, mean=1.7). Agonistic interactions were very rare (see results), so statistical analyses were not possible.

Collection and analysis of demographic data

We estimated the relationship between harem size and individual survival using data from the long-term sight-resight study. Twice a year, during approximately one month in the wet season and three weeks in the dry season, groups whose individuals were known were sought. When found, harem size and identity of the individuals were recorded. The age of previously unobserved young individuals was estimated as in Grange et al. (2015) and suckling used to

determine motherhood. Further details on the monitoring of this population can be found in Grange et al. (2015). Data collected between January 2008 and March 2017 were used here, corresponding to 19 capture occasions (10 wet and 9 dry seasons) over 10 years.

We used multistate CMR models to estimate adult survival (Lebreton et al. 2009). CMR modelling allowed us to account for the fact that not all known individuals were observed at each session (imperfect detection). States were used to represent group size classes: small, medium and large for harems of size 2 to 3, 4 to 5, and 6 and more, respectively. Foals were not used for the calculation of group size. This classification was chosen based on the distribution of harem sizes in the population (Fig. 1). Using a different categorization of group sizes did not change our results (Appendix S1: Tables S1-S4) and classifying group sizes into more states created too many parameters for our models. See supporting information for further details on encounter histories and survival, detection and transition matrices (Appendix S2: Figs. S1-S3). We ran separate models for females and males. We added a fourth state in the male analysis to represent their presence in bachelor group (whose group size was usually not recorded). A total of 143 females and 105 males were retained for analysis. The U-CARE software (Choquet et al. 2009) was first used to perform goodness-of-fit tests to identify any issues in the structure of our datasets (Pradel et al. 2003). Models were fitted using the R package *RMark* (Laake 2013), starting from a full model including an interactive effect of group size and season on survival probability, an additive effect of group size and season on detection probability, and a group size effect on transition probability. As our goal was to see how group size affects survival, we created only three simpler models from this model, which included either a season effect, a group size effect, or an additive effect of season and group size on the survival probability of adults. We used AICc to select the most parsimonious model, considering only informative parameters (Arnold 2010). Estimates were corrected for unequal time intervals between capture occasions. Each interval was defined as the time from the start of the field session until the start of the following field session.

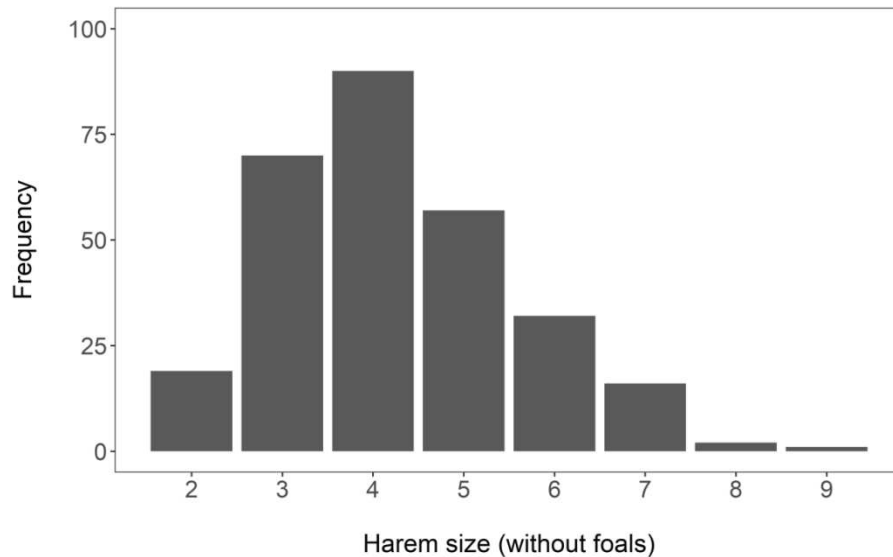


Figure 1. Distribution of harem sizes (without foals) across sightings (median=4, mean=4.26, 1st Qu=3, 3rd Qu=5).

For foals (less than 1 y.o.), we used the fact that they are dependent on their mother. If the mother was observed, the detection probability of the foal being alive is 1, and the observation of a mare without her foal is reliable evidence that the foal had not survived. We therefore used standard Cox proportional-hazards models, fitted with the R package *survival* (Therneau 2020). A total of 114 foals were retained for the analysis. Due to small sample sizes, we could not test for the effect of season on foal survival, so we restricted our analysis to two models which included either an effect of age-at-entry (i.e. estimated age in days when they were first observed) or an additive effect of group size and age-at-entry on the survival probability of foals. As age-at-entry for foals were highly variables (min=0, max=334, median=46, mean=68.7), we choose to run a time-on-study model which is more robust to variations in age-at-entry than the chronological age one (Chalise et al. 2012). Age-at-entry was therefore included as a 2-class variable (0-1 and 1-6 months-old).

RESULTS

Effect of group size on behavior

The duration of vigilance bouts was not affected, either linearly or curvilinearly, by group size in isolated harems (Fig. 2; Appendix S3: Table S1). In herds, aggregation of groups that were usually larger than single harems, vigilance decreased with group size during the wet season, but increased with group size during the dry season (Fig. 2; Appendix S3: Table S1). Vigilant bouts were on average slightly longer in the dry season (Fig. 2).

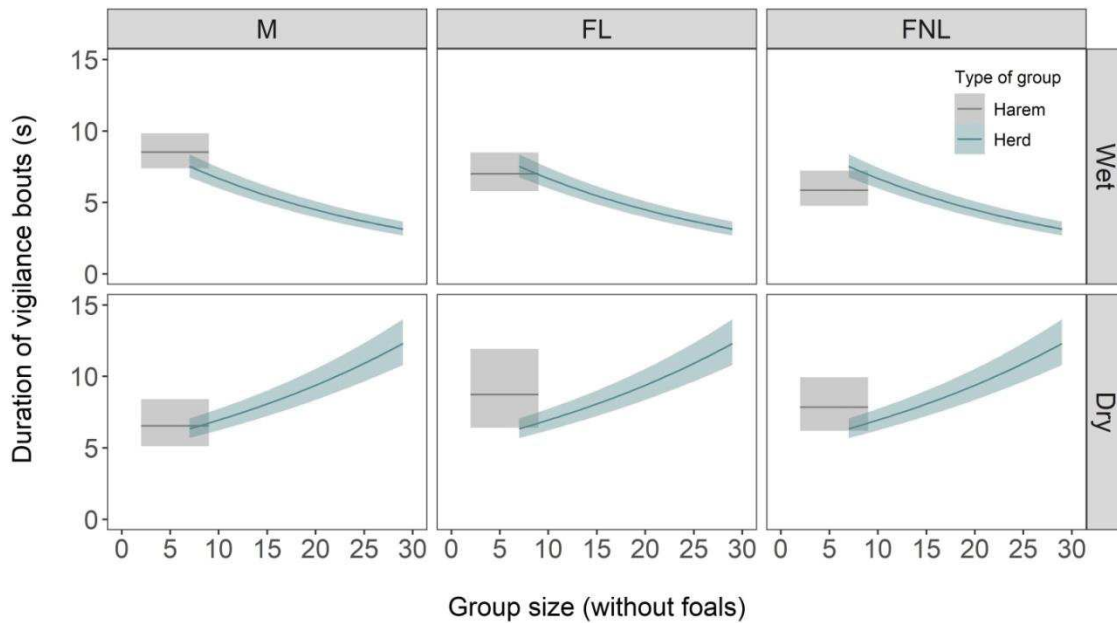


Figure 2. Duration of vigilance bouts in relation to group size (without foals), for males (M), lactating females (FL) and non-lactating females (FNL) in wet and dry seasons. Model predictions and 95% confidence envelopes are shown.

The duration of foraging bouts was affected linearly by group size in isolated harems, decreasing with group size in males and increasing with group size in lactating females (Fig. 3; Appendix S3: Table S2). Group size had no influence on the duration of foraging bouts in herds (Fig. 3; Appendix S3: Table S2). Foraging bouts were on average slightly shorter during the dry season (Fig. 3).

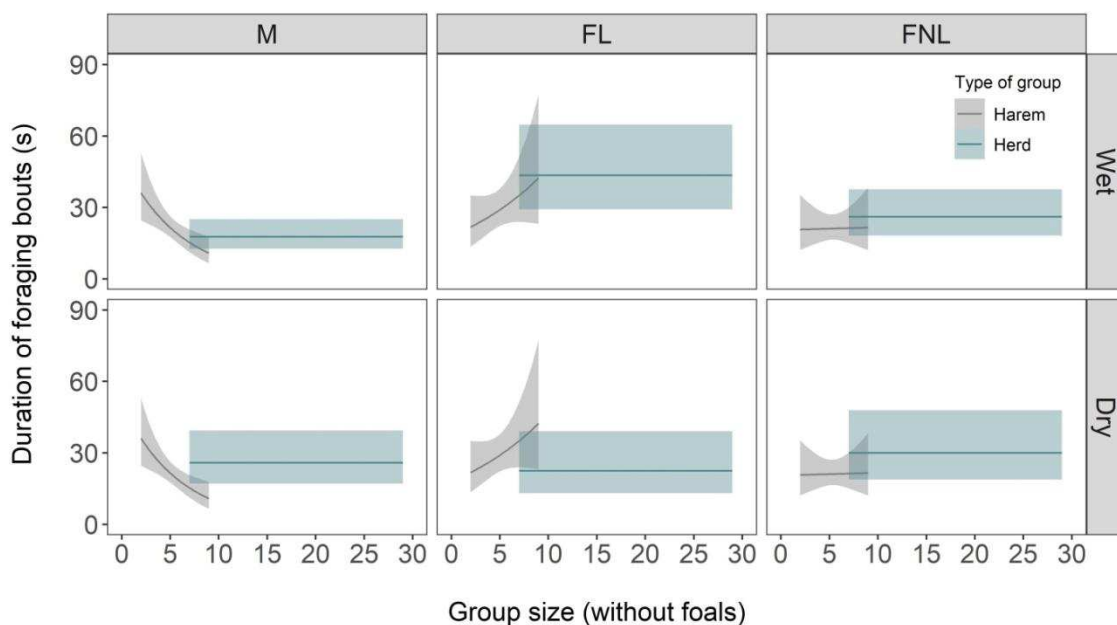


Figure 3. Duration of foraging bouts in relation to group size (without foals), for males (M), lactating females (FL) and non-lactating females (FNL) in wet and dry seasons. Model predictions and 95% confidence envelopes are shown.

The likelihood that at least one individual of the group was vigilant increased strongly with group size, both in isolated harems and in herds (Fig. 4; Appendix S3: Table S3), with no seasonal differences.

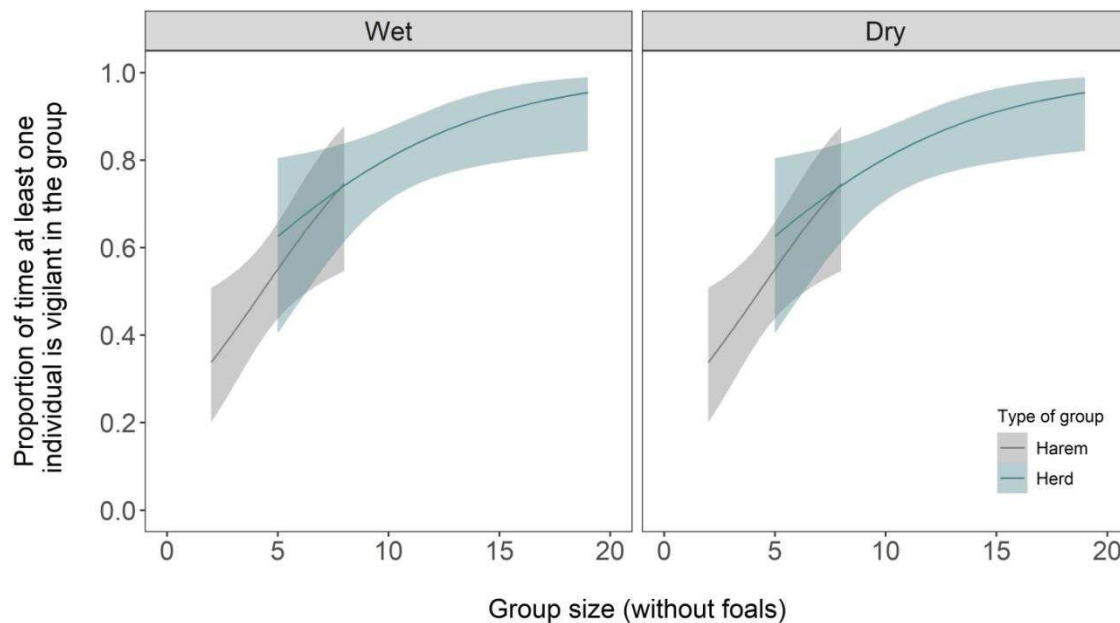


Figure 4. Proportion of times at least one individual is vigilant in the group in relation to group size (without foals) in wet and dry seasons. Model predictions and 95% confidence envelopes are shown.

Agonistic interactions were very rare. Over 636 foraging bouts observed, only 1 was interrupted by an agonistic interaction. When zebras were travelling or resting, agonistic interactions were also low. We observed only 7 and 13 agonistic interactions (AI) during 0.77 h and 5.33 h when zebras were travelling (9.1 AI h^{-1}) and resting (2.4 AI h^{-1}) respectively : 30% were threats (least intense level of agonism), 20% were pushes, and 50% were attacks (these involved physical contacts but rarely lead to severe injuries).

Effect of harem size on survival

Data for adult males did not show any lack of fit ($X^2(146) = 89.182$, $p = 1$). However, we found evidence for a lack of fit in adult females' data ($X^2(142) = 232.505$, $p = 0$), apparently due to a transient effect (test 3G.SR: $X^2(26) = 58.331$, $p = 0$). We therefore corrected AICc values for over-dispersion (coefficient = 1.5015).

The survival of both adult males and females changed between seasons but was not affected by harem size (Table 1). Adult male survival was $0.863 (\pm 0.027 \text{ SE}, 95\% \text{ CI } [0.801-0.908])$ in the wet season and $0.926 (\pm 0.022 \text{ SE}, 95\% \text{ CI } [0.870-0.959])$ in the dry season. Adult female

survival was 0.935 (± 0.022 SE, 95% CI [0.877-0.967]) in the wet season and 0.881 (± 0.020 SE, 95% CI [0.836-0.915]) in the dry season.

Table 1. Statistics for models of adult survival. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for adults. Bold lettering indicates the selected models. # Models for adult females are classified using the Akaike Information Criterion corrected for over-dispersion (QAICc, Δ -QAICc and QDeviance). Effects tested on survival, detection, and transition probabilities are group size (gs) and season (s).

	Survival	Detection	Transition	n	AICc [#]	Δ -AICc [#]	Deviance [#]
Adult males	s	$gs+s$	gs	19	1749.94	0.00	1539.38
	gs	$gs+s$	gs	21	1752.26	2.32	1537.32
	$gs+s$	$gs+s$	gs	22	1752.28	2.34	1535.14
	$gs*s$	$gs+s$	gs	25	1753.14	3.20	1529.33
Adult females	s	$gs+s$	gs	12	1631.73	0.16	1382.76
	gs	$gs+s$	gs	13	1631.58	0.00	1380.52
	$gs+s$	$gs+s$	gs	14	1632.07	0.49	1378.93
	$gs*s$	$gs+s$	gs	16	1635.63	4.06	1378.31

The survival of foals was not clearly affected by harem size. The model including harem size effect was only 2.84 AIC units better than the model without this factor, while having two extra parameters should have reduced AIC by four to be considered informative (Table 2). Survival estimates from the models including harem size were lower in medium-sized harems than in smaller or larger ones (Appendix S4: Table S1).

Table 2. Statistics for models of foal survival. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for foals. Bold lettering indicates the selected model. Effects tested on survival probabilities are group size (gs) and age-at-entry (a).

	Model	n	AICc	Δ -AICc	Deviance
Foals	Survival $\sim gs + a$	3	404.06	0.00	397.90
	Survival $\sim a$	1	406.90	2.84	404.88

DISCUSSION

This study shows that group size does not have large and consistent effects on plains zebra vigilance or foraging behaviors at the individual level. This is despite the fact that group size increases the likelihood of not being targeted if attacked (dilution effect), and the likelihood of having at least one vigilant individual at any time, which should facilitate collective vigilance in larger groups. We found that agonistic interactions were rare. Overall, this suggests that in plains zebras increasing group size comes with little benefits or costs linked to foraging and vigilance. Accordingly, the size of the most stable unit, the harem, has no straightforward effect on survival, even in context of high predation pressure.

Lack of, or inconsistency of, group size effects on vigilance and foraging

Contrary to our predictions, we found no consistent effect of group size on the duration of either vigilance or foraging bouts. Group size did contribute to an explanation of these variables in a few instances, but this effect was not always consistent with the decrease expected from a dilution or detection effect, was most often not large, or was driven by what happens in uncommon situations (i.e. very large group size). For instance, zebras had shorter vigilance bouts when in very large herds, but this was true only in the wet season. The occurrence of such large aggregations was rare. The only situation in which foraging bouts increased with group size was for lactating females, and this effect did not persist in larger herds. Therefore, our results suggest that group size has little effect on individual vigilance and foraging in plains zebras at our study site. This view is supported by the inconsistent results on the relationship between group size and vigilance and foraging found by previous independent studies conducted in the same species, either at the same site (Périquet et al. 2010, 2012, Barnier et al. 2016) or elsewhere (Schmitt et al. 2014, Périquet et al. 2017). Thus, we conclude that we found no evidence of biologically significant detection or dilution effects on the duration of vigilance and foraging bouts.

We see three possible explanations for this unexpected result: (1) dilution or collective detection don't occur or are not relied upon by zebras. Although zebra group sizes are generally small, this is the situation in which the dilution effect, a $1/N$ effect, should be strongest. However, several conditions are required for dilution to occur. First, the rate of attacks by predators should not increase with increasing group size (Turner and Pitcher 1986). If this is so, individuals in smaller groups should benefit from increased safety (Creel and Winnie 2005), unlike what is predicted by the dilution and detection effects. In HNP, larger zebra groups could be more conspicuous and more frequently attacked by lions. This hypothesis cannot be tested at the moment. Secondly, dilution effects are expected to fade if predators attack a subset of individuals

in groups of prey more frequently. Lions have been shown to preferentially attack zebra foals in Kruger National Park and Etosha National Park (Stander 1992, Mills and Shenk 1992) and this is likely the case in HNP too. If so, group size becomes a poor indicator of the level of risk experienced by individuals and the risk of being predated will likely be decoupled from the size of the group. This is also the case if individuals at the periphery of groups are preferentially targeted (the geometry of the selfish herd, Hamilton 1971), although our data do not suggest that individuals at the periphery are more vigilant (not shown). We also acknowledge that, although the dilution effect has until now been looked, like here, at the scale of the group, it may actually operate first and foremost at a higher scale: for instance at the scale of the predator's foraging patch where groups, not individuals, can dilute each other's risk. Therefore, there are reasons why dilution at the group scale might not occur. Regarding collective detection, our results show that larger groups make it more likely to have at least one vigilant individual at any time. However, this probability remains significantly lower than 1.0 at most group sizes, and therefore individuals may be reluctant to rely on this effect. Also, it is known that it can be risky to rely on vigilance by another individual, as this one may be more likely to escape attack than non-vigilant individuals, which are more likely to become the predator's target (Bednekoff and Lima 1998). This process explains why vigilance coordination is rarely observed in systems without dedicated sentinels (Pays et al. 2007b, 2007c, 2012). There is also no evidence of vigilance coordination in zebras at our study site (unpublished study), suggesting that they might not rely on collective vigilance. Another possible explanation is that (2) zebras in larger groups may, if group size reduces risk, trade off this safety not for reduced vigilance but for greater use of riskier patches of higher forage quality. At the study site, larger groups of zebras may use riskier, but possibly richer, patches (Patin 2018), and such group size dependent space-use adjustments to predation risk might invalidate the traditional expectations about the group size - vigilance relationship (Patin et al. 2019). A third possibility is that (3) the prediction that dilution and collective detection should lead to reduce individual vigilance is based on the assumption that vigilance reduces foraging rate. This might not be the case here. Indeed, 90 % of the vigilance bouts observed were free vigilance bouts, as zebra chew the previous bite while being vigilant. If vigilance and foraging are not mutually exclusive activities, zebras do not have to trade-off foraging for vigilance as they can perform both simultaneously and this could explain why individuals in larger groups did not reduce their vigilance level.

Overall, many explanations, some not mutually exclusive, can be brought forward to explain the lack of a consistent vigilance - group size relationship in these plains zebras, and likely in other species. Future work is needed to clarify whether or not they hold true. It will be

challenging to do this in the wild, and modelling work might be helpful to narrow the field of investigation initially. Whatever the underlying reason(s), we did not find that increasing group size improve foraging rates in plains zebras.

Lack of evidence for costs dependent on group size via interference and agonistic interactions

Contrary to our prediction, we found no apparent costs related to intra-group interference competition for access to resources in our study population. Agonistic interactions were rare, as found in other plains zebra populations (Fischhoff et al. 2009, Simpson et al. 2012). Due to this rarity, we could not test our hypothesis that the frequency of agonistic interactions increases as group size increases. However, foraging plains zebras were rarely interrupted by agonistic interactions, so our results suggest that intra-group competition could have at most only a weak impact on the cost-benefit balance of grouping for these zebras.

Lack of evidence for a survival effect of harem size

We did not find evidence that harem size affects the survival of individuals in this population in which individuals experience high predation risk. This is consistent with our behavioral observation suggesting no clear effect of group size on vigilance and foraging behavior. Some other benefits and costs of group living do exist and were not considered here (e.g. costs related to behavioral synchrony and decision-making, parasitism). Our results however show that, irrespective of the mechanisms considered, harem size has no overriding influence on survival, a pattern found in some of the few similar studies conducted on non-cooperative breeding species under predation (Robinson 1988, Brown et al. 2016). We could not study whether grouping at higher social levels, i.e. between harems, has fitness benefits. The frequency of such associations remains unknown and would be difficult to estimate in the field. However, an adaptive perspective of the instability of these multi-harem herds suggests that the costs and benefits of such groupings must be highly time and space dependent and further research on their social and ecological determinants is clearly needed.

CONCLUSION

In conclusion, this study provides a rare comprehensive test of the demographic relevance of dilution and detection effects under predation risk, by combining behavioral observations and long-term demographic data. The results show that group size does not have an effect on vigilance, as has been found in some other studies (Treves 2000, Beauchamp 2008). Most importantly, all these results question whether fitness benefits of dilution or detection should

always be assumed, as is commonly done in many empirical and theoretical works (e.g. Serrano et al. 2005, Lehtonen and Jaatinen 2016, Guindre-Parker and Rubenstein 2020). We argue that further studies on group size - fitness relationships are needed, particularly on species which do not breed cooperatively. This would allow a stronger conceptual framework for understanding how predation shapes animal sociality to be built.

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APPENDIX S1

We tested if categorizing harem sizes into different classes changed the selection of survival models. We tested two other classifications of harem sizes : (1) harems with 2 to 3, 4 to 6, and 7 and more individuals were classified as small, medium and large respectively (Tables S1-S2), and (2) harems with 2 to 3, 4, and 5 and more individuals were classified as small, medium and large respectively (Tables S3-S4). The comparison showed that the way we categorized group size did not affect our results qualitatively.

Table S1. Statistics for models of adult survival; harem sizes with 2 to 3, 4 to 6, and 7 and more individuals are classified as small, medium and large respectively. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for adults. Bold lettering indicates the selected models. # Models for adult females are classified using the Akaike Information Criterion corrected for over-dispersion (QAICc, Δ -QAICc and QDeviance). Effects tested on survival, detection and transition probabilities are group size (gs) and season (s).

	Survival	Detection	Transition	n	AICc [#]	Δ -AICc [#]	Deviance [#]
Adult males	s	$gs+s$	gs	19	1653.34	0.00	1437.05
	$gs+s$	$gs+s$	gs	22	1656.32	2.98	1433.45
	$gs*s$	$gs+s$	gs	25	1657.09	3.75	1427.55
	gs	$gs+s$	gs	21	1657.12	3.78	1436.45
Adult females	s	$gs+s$	gs	12	1491.79	0.00	1231.47
	gs	$gs+s$	gs	13	1492.35	0.56	1229.95
	$gs+s$	$gs+s$	gs	14	1493.10	1.31	1228.62
	$gs*s$	$gs+s$	gs	16	1496.61	4.83	1227.95

Table S2. Statistics for models of foal survival; harem sizes with 2 to 3, 4 to 6, and 7 and more individuals are classified as small, medium and large respectively. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for foals. Bold lettering indicates the selected model. Effects tested on survival probabilities are group size (gs) and age-at-entry (a).

	Model	n	AICc	Δ -AICc	Deviance
Foals	Survival $\sim a$	1	406.90	0.00	404.88
	Survival $\sim gs + a$	3	407.05	0.15	400.90

Table S3. Statistics for models of adult survival; harem sizes with 2 to 3, 4, and 5 and more individuals are classified as small, medium and large respectively. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for adults. Bold lettering indicates the selected models. # Models for adult females are classified using the Akaike Information Criterion corrected for over-dispersion (QAICc, Δ -QAICc and QDeviance). Effects tested on survival, detection and transition probabilities are group size (gs) and season (s).

	Survival	Detection	Transition	n	AICc [#]	Δ -AICc [#]	Deviance [#]
Adult males	s	$gs + s$	gs	19	1767.73	0.00	1564.29
	$gs + s$	$gs + s$	gs	22	1768.02	0.30	1558.02
	gs	$gs + s$	gs	21	1768.94	1.22	1561.14
	$gs * s$	$gs + s$	gs	25	1769.30	1.58	1552.63
Adult females	s	$gs + s$	gs	12	1611.60	0.24	1366.18
	gs	$gs + s$	gs	13	1611.36	0.00	1363.86
	$gs + s$	$gs + s$	gs	14	1612.35	0.99	1362.77
	$gs * s$	$gs + s$	gs	16	1615.57	4.20	1361.80

Table S4. Statistics for model of foal survival; harem sizes with 2 to 3, 4, and 5 and more individuals are classified as small, medium and large respectively. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, and deviance for the models fitted for foals. Bold lettering indicates the selected model. Effects tested on survival probabilities are group size (gs) and age-at-entry (a).

	Model	n	AICc	Δ -AICc	Deviance
Foals	Survival $\sim gs + a$	3	406.60	0.00	400.44
	Survival $\sim a$	1	406.90	0.30	404.88

APPENDIX S2

We constructed encounter histories for all individuals based on initial observations of zebras and subsequent observations in the following capture occasions and the size/type of its group. We censored the encounter histories of individuals with “.” whenever we knew they were dead. In the CMR analysis, adult males and females could be observed in 5 different states {present in a small-size harem (state 1), present in a medium-size harem (state 2), present in a large-size harem (state 3), present in a bachelor group (state 4) (only for adult males), or dead (†)}. Therefore, encounter histories were coded with 6 events at each capture occasions {not observed (0), observed in a small-size harem (1), observed in a medium-size harem (2), observed in a large-size harem (3), observed in a bachelor group (4), or dead (.)}. For instance, an individual with encounter history ‘40021’ is an individual that was seen in a bachelor group at first occasion, not observed during the two following sessions, observed on the fourth occasion in a medium-size harem, and then seen on the fifth occasion in a small-size harem.

<i>t</i> +1 :	state 1	state 2	state 3	state 4	†	
<i>t</i>						
state 1	S_1	0	0	0	$1 - S_1$	= <i>S</i>
state 2	0	S_2	0	0	$1 - S_2$	
state 3	0	0	S_3	0	$1 - S_3$	
state 4	0	0	0	S_4	$1 - S_4$	
†	0	0	0	0	1	

Figure S1. Survival matrix for adults. Grey row and column relate to adult males only.

	0	1	2	3	4	.	
states							
state 1	$1 - P_1$	P_1	0	0	0	0	= <i>p</i>
state 2	$1 - P_2$	0	P_2	0	0	0	
state 3	$1 - P_3$	0	0	P_3	0	0	
state 4	$1 - P_4$	0	0	0	P_4	0	
†	1	0	0	0	0	0	

Figure S2. Detection matrix for adults. Grey row and column relate to adult males only.

$t+1 :$	state 1	state 2	state 3	state 4	†	
t						
state 1	ψ_{11}	ψ_{12}	ψ_{13}	ψ_{14}	0	= ψ
state 2	ψ_{21}	ψ_{22}	ψ_{23}	ψ_{24}	0	
state 3	ψ_{31}	ψ_{32}	ψ_{33}	ψ_{34}	0	
state 4	ψ_{41}	ψ_{42}	ψ_{43}	ψ_{44}	0	
†	0	0	0	0	1	

Figure S3. Transition matrix for adults. Grey row and column relate to adult males only.

APPENDIX S3

We identified models with most support from the data using an AICc-based model selection. Number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), Δ -AICc, deviance, and marginal R-squared values (R^2m) are shown.

Table S1. Duration of vigilance bouts in relation to group size (gs), season (s), a variable coding for sex and reproductive status ($sxrp$), and other variables known to potentially affect vigilance ($\#$). Bold lettering indicates the selected models.

	Model †	n	AICc	Δ -AICc	Deviance	R^2m
Harem	Vigilance ~ $sxrp * s + \#$	17	977.04	0.00	939.04	0.19
	Vigilance ~ $gs + sxrp * s + \#$	18	979.16	2.13	938.66	0.16
	Vigilance ~ $\text{poly}(gs,2) + sxrp * s + \#$	19	981.61	4.57	938.58	0.16
	Vigilance ~ $gs + sxrp + s + \#$	16	982.28	5.24	946.74	0.11
	Vigilance ~ $gs * s + sxrp + \#$	17	984.41	7.37	946.40	0.11
	Vigilance ~ $\text{poly}(gs,2) + sxrp + s + \#$	17	984.73	7.69	946.72	0.11
	Vigilance ~ $gs * sxrp + s + \#$	18	987.18	10.14	946.68	0.11
	Vigilance ~ $gs * sxrp * s + \#$	23	988.73	11.69	935.22	0.18
	Vigilance ~ $\text{poly}(gs,2) * s + sxrp + \#$	19	989.19	12.15	946.16	0.12
	Vigilance ~ $\text{poly}(gs,2) * sxrp + s + \#$	21	992.89	15.86	944.70	0.12
	Vigilance ~ $\text{poly}(gs,2) * sxrp * s + \#$	29	1002.89	25.85	932.54	0.19
Herd	Vigilance ~ $\text{poly}(gs,2) * s + sxrp + \#$	19	686.81	0.00	640.46	0.17
	Vigilance ~ $gs * s + sxrp + \#$	17	688.24	1.43	647.66	0.10
	Vigilance ~ $gs + sxrp + s + \#$	16	690.32	3.50	652.52	0.06
	Vigilance ~ $sxrp * s + \#$	17	690.70	3.89	650.12	0.08
	Vigilance ~ $\text{poly}(gs,2) + sxrp + s + \#$	17	691.96	5.15	651.38	0.07
	Vigilance ~ $gs * sxrp + s + \#$	18	693.42	6.60	649.98	0.08
	Vigilance ~ $gs + sxrp * s + \#$	18	693.45	6.63	650.02	0.08

Table S1. (Continued)

Model †	<i>n</i>	AICc	Δ-AICc	Deviance	R ² m
Vigilance ~ poly(<i>gs</i> ,2) + <i>sxrp</i> * <i>s</i> + #	19	695.31	8.50	648.96	0.09
Vigilance ~ <i>gs</i> * <i>sxrp</i> * <i>s</i> + #	23	698.97	12.16	640.28	0.16
Vigilance ~ poly(<i>gs</i> ,2) * <i>sxrp</i> + <i>s</i> + #	21	699.00	12.19	646.62	0.11
Vigilance ~ poly(<i>gs</i> ,2) * <i>sxrp</i> * <i>s</i> + #	29	710.64	23.82	631.16	0.24

Other_sp + *Foraging* + *Dist_cov* + *Dist_obs* + *Grass* + *Wind* + (1|*ID*) + (1|*ObsID*)

† *Vigilance* = duration of the vigilance bout (in seconds), *gs* = size of the group (without foals), *sxrp* = sex and reproductive status of the individual (*M* for males, *FNL* for non-lactating females and *FL* for lactating females), *s* = season, *Other_sp* = presence/absence of other species within 50 m around the focal harem, *Foraging* = duration of the foraging bout that precedes the vigilance bout (in seconds), *Dist_cov* = distance to cover (in meters), *Dist_obs* = distance to observer (in meters), *Grass* = vegetation height (small, medium or tall), *Wind* = wind strength (none, low, medium or strong), (1|*ID*) = identity of the individual as random effect, (1|*ObsID*) = identity of the focal as random effect.

Table S2. Duration of foraging bouts in relation to group size (*gs*), season (*s*), a variable coding for sex and reproductive status (*sxrp*), and other variables known to potentially affect foraging (#). Bold lettering indicates the selected models.

	Model †	<i>n</i>	AICc	Δ-AICc	Deviance	R ² m
Harem	Foraging ~ <i>gs</i> * <i>sxrp</i> + <i>s</i> + #	18	1545.71	0.00	1505.18	0.20
	Foraging ~ poly(<i>gs</i> , 2) * <i>sxrp</i> + <i>s</i> + #	21	1547.89	2.18	1499.47	0.23
	Foraging ~ <i>gs</i> + <i>sxrp</i> + <i>s</i> + #	16	1550.96	5.25	1505.41	0.15
	Foraging ~ <i>gs</i> * <i>sxrp</i> * <i>s</i> + #	23	1551.43	5.72	1497.87	0.23
	Foraging ~ <i>sxrp</i> * <i>s</i> + #	17	1551.89	6.17	1513.86	0.15
	Foraging ~ poly(<i>gs</i> , 2) + <i>sxrp</i> + <i>s</i> + #	17	1552.53	6.81	1514.50	0.15
	Foraging ~ <i>gs</i> + <i>sxrp</i> * <i>s</i> + #	18	1552.82	7.10	1512.29	0.16
	Foraging ~ <i>gs</i> * <i>s</i> + <i>sxrp</i> + #	17	1552.94	7.22	1514.91	0.15
	Foraging ~ poly(<i>gs</i> , 2) + <i>sxrp</i> * <i>s</i> + #	19	1553.85	8.14	1510.78	0.17

Table S2. (Continued)

	Model †	<i>n</i>	AICc	Δ-AICc	Deviance	R ² m
	Foraging ~ poly(<i>gs</i> , 2) * <i>s</i> + <i>sxrp</i> + #	19	1557.42	11.70	1514.35	0.15
	Foraging ~ poly(<i>gs</i> , 2) * <i>sxrp</i> * <i>s</i> + #	29	1561.05	15.33	1490.62	0.27
Herd	Foraging ~ <i>sxrp</i> * <i>s</i> + #	17	1036.30	0.00	995.72	0.22
	Foraging ~ <i>gs</i> * <i>s</i> + <i>sxrp</i> + #	17	1037.89	1.59	997.31	0.21
	Foraging ~ <i>gs</i> + <i>sxrp</i> * <i>s</i> + #	18	1038.90	2.60	995.47	0.22
	Foraging ~ <i>gs</i> + <i>sxrp</i> + <i>s</i> + #	16	1039.00	2.70	1001.22	0.18
	Foraging ~ poly(<i>gs</i> , 2) + <i>sxrp</i> * <i>s</i> + #	19	1039.94	3.63	993.58	0.24
	Foraging ~ poly(<i>gs</i> , 2) + <i>sxrp</i> + <i>s</i> + #	17	1040.12	3.81	999.54	0.19
	Foraging ~ poly(<i>gs</i> , 2) * <i>s</i> + <i>sxrp</i> + #	19	1042.52	6.22	996.17	0.22
	Foraging ~ <i>gs</i> * <i>sxrp</i> * <i>s</i> + #	23	1042.66	6.36	983.97	0.31
	Foraging ~ <i>gs</i> * <i>sxrp</i> + <i>s</i> + #	18	1043.20	6.90	999.77	0.19
	Foraging ~ poly(<i>gs</i> , 2) * <i>sxrp</i> + <i>s</i> + #	21	1047.72	11.41	995.34	0.23
	Foraging ~ poly(<i>gs</i> , 2) * <i>sxrp</i> * <i>s</i> + #	29	1059.59	23.28	980.11	0.34

Others_sp + *Vigilance* + *Dist_cov* + *Dist_obs* + *Grass* + *Wind* + (1|*ID*) + (1|*ObsID*)

† Foraging = duration of the foraging bout (in seconds), *gs* = size of the group (without foals), *sxrp* = sex and reproductive status of the individual (*M* for males, *FNL* for non-lactating females and *FL* for lactating females), *s* = season, *Other_sp* = presence/absence of other species within 50 m around the focal harem, *Vigilance* = duration of the vigilance bout that precedes the foraging bout (in seconds), *Dist_cov* = distance to cover (in meters), *Dist_obs* = distance to observer (in meters), *Grass* = vegetation height (small, medium or tall), *Wind* = wind strength (none, low, medium or strong), (1|*ID*) = identity of the individual as random effect, (1|*ObsID*) = identity of the focal as random effect.

Table S3. Proportion of times at least one individual is vigilant in the group in relation to group size (gs), season (s) and other variables known to potentially affect vigilance ($\#$). Bold lettering indicates the selected models.

	Model †	n	AICc	Δ -AICc	Deviance	R^2_m
Harem	Prop_1vig ~ $gs + \#$	11	290.46	0.00	264.27	0.12
	Prop_1vig ~ $gs + s + \#$	12	292.54	2.08	263.51	0.12
	Prop_1vig ~ poly($gs,2$) + $\#$	12	293.17	2.72	264.14	0.12
	Prop_1vig ~ $gs * s + \#$	13	295.38	4.92	263.42	0.12
	Prop_1vig ~ poly($gs,2$) + $s + \#$	13	295.44	4.98	263.47	0.12
	Prop_1vig ~ $s + \#$	11	296.03	5.57	269.84	0.06
	Prop_1vig ~ poly($gs,2$) * $s + \#$	15	299.18	8.72	261.05	0.13
Herd	Prop_1vig ~ gs	2	49.94	0.00	45.24	0.08
	Prop_1vig ~ poly($gs,2$)	3	52.64	2.70	45.14	0.07
	Prop_1vig ~ $gs + s$	3	52.65	2.71	45.15	0.08
	Prop_1vig ~ s	2	54.78	4.84	50.08	0.02
	Prop_1vig ~ $gs * s$	4	55.52	5.58	44.86	0.09
	Prop_1vig ~ poly($gs,2$) + s	4	55.75	5.81	45.09	0.07
	Prop_1vig ~ poly($gs,2$) * s	6	62.55	12.61	44.09	0.14

#Others_sp + Dist_cov + Dist_obs + Grass + Wind + (1|GroupID)

† Prop_1vig = number of times at least one individual is vigilant in the group / number of times none of the individuals in the group is vigilant, gs = size of the group (without foals), s = season, Other_sp = presence/absence of other species within 50 m around the focal harem, Dist_cov = distance to cover (in meters), Dist_obs = distance to observer (in meters), Grass = vegetation height (small, medium or tall), Wind = wind strength (none, low, medium or strong), (1|GroupID) = identity of the group as random effect.

APPENDIX S4

Table S1. Estimates, standard errors (SE), 95% confidence intervals and p-values for the Cox proportional-hazards model fitted for foals including an additive effect of group size and age-at-entry on foal survival.

Parameter	Estimate	SE	Lower 95%	Upper 95%	P-value
Group size class : medium	0.28	0.35	0.66	2.64	0.43
Group size class : large	-0.54	0.51	0.22	1.58	0.29
Age class : 1-6 months	-0.37	0.29	0.39	1.23	0.21

CHAPITRE 2

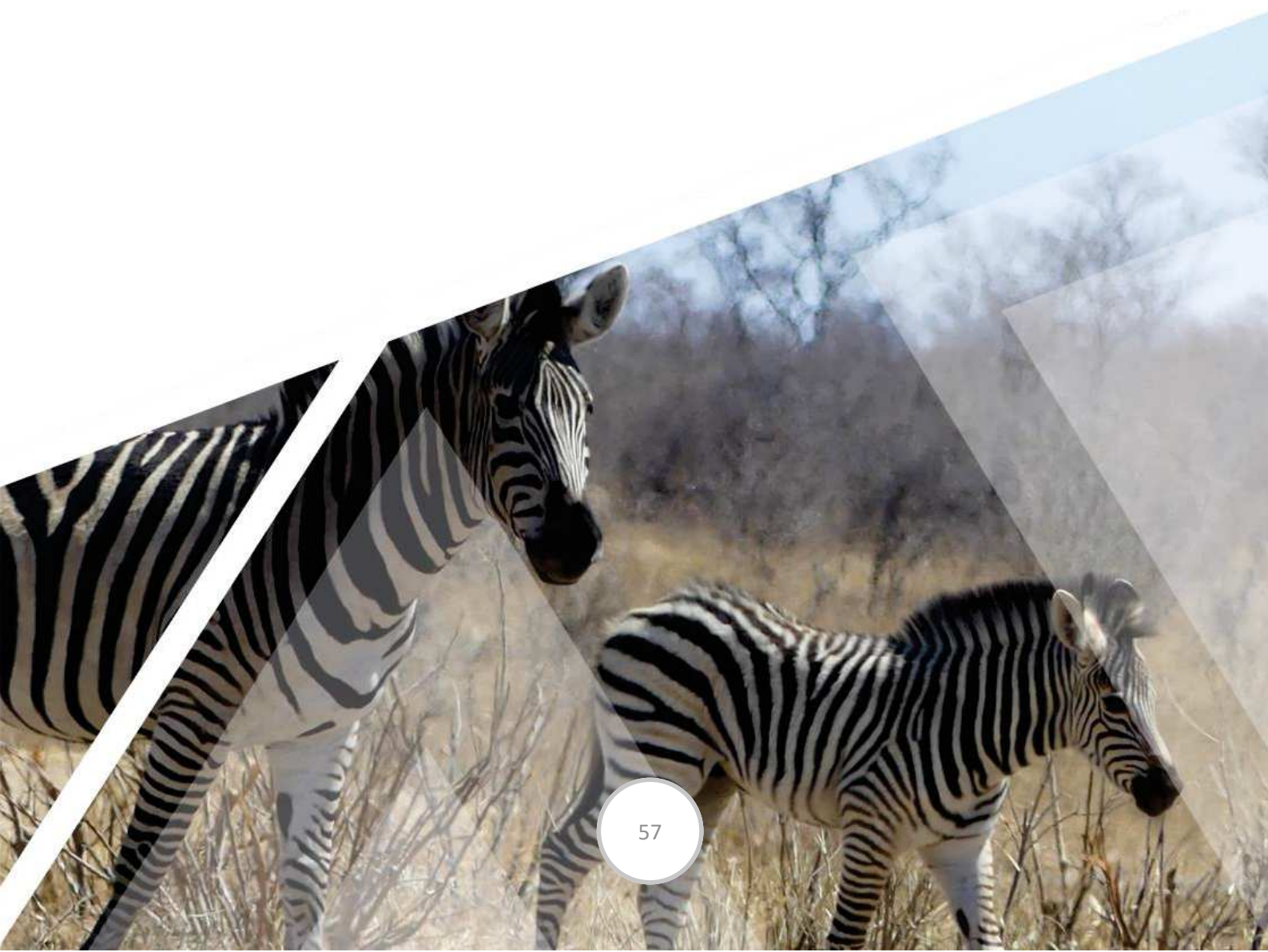
Do infanticides occur in harem-forming equids?

A test with long-term socio-demographic data in wild plains zebras

Les comportements d'infanticides existent-ils chez les équidés formant des harems ? Un test avec des données socio-démographiques collectées sur le long terme chez le zèbre des plaines en milieu sauvage

Camille Vitet, Patrick Duncan, Andre Ganswindt, Cheryl Mabika, Simon Chamaillé-Jammes

Article soumis chez Animal Behaviour



ABSTRACT

The population consequences of social dynamics are often questioned, as for instance in species known or believed to experience infanticide when a dominant male is replaced by another. Infanticide by males has been observed in many taxa, mostly in species that breed year round and in which a few males monopolize reproduction. In such species, infanticide often occurs after takeovers of breeding groups, and the frequency of takeovers often increases with increasing female group size, therefore raising the risk of infanticide in larger groups. Among ungulates, male infanticide has been reported mostly in harem-forming equids in captive populations, usually following harem-male turnover. In this study, we empirically tested in the wild whether the rate of stallion (i.e. harem-male) turnover increases with the number of reproductive females in harems, and whether these events reduce foal survival. We used a long-term study of wild plains zebra *Equus quagga* of Hwange National Park, Zimbabwe, where, for more than 15 years, stallion turnovers were recorded and accurate data on pregnancy were obtained by hormone assays. We show that stallion turnovers are frequent and, as expected, particularly in harems with a large number of reproductive females. We then show that foal survival did not differ significantly between situations when a stallion turnover occurred shortly before or after their birth and when it did not. This result was consistent with the fact that no attacks by stallions on foals of their group or forced matings were observed during the study. Our study offers rare data showing that if male infanticide occurs in wild plains zebra, this should be extremely rare, and has no important consequences for foal survival at the population level.

KEYWORDS: equids, group size, infant mortality, male turnover, sociality

INTRODUCTION

The population consequences of social dynamics are often questioned (Clutton-Brock 2016). Interactions between conspecifics can directly affect their fitness: to the extreme, some individuals can kill or be killed, as for instance in several mammalian carnivores during territorial conflicts (Mech 1994, Mosser and Packer 2009, Thompson et al. 2017). More commonly, individuals can affect the reproductive output of others via various social behaviours, for instance, by limiting access to resources (e.g. interference competition) or mates (e.g. intra-sexual competition), or, in contrast, by taking care of one's offspring (e.g. communal breeding) (Silk 2007).

A classic example of such link between social dynamics and individuals' fitness is infanticide by males - the killing of dependent offspring by an unrelated conspecific adult male - which is widespread, occurring in taxa as varied as fish, amphibians, birds, and mammals (Hausfater and Hrdy 1984, Lukas and Huchard 2014). Obviously, an infanticide decreases the reproductive output of the female whose offspring is killed. Conversely, the reproductive output of the infanticidal male is likely increased: the most commonly accepted hypothesis for the evolution of this behaviour, the 'sexual selection hypothesis', posits that an infanticidal male increases its mating opportunities by shortening the latency during which a female is unavailable to reproduce, either because of temporal infertility or behavioural rejection of mating attempts (Hrdy 1979, McNeilly 1997, Dixson 2012).

The importance of infanticide by males, as a factor shaping population dynamics, remains controversial however. Previous works on rodents have shown that population growth rates can be dramatically reduced when the rate of male replacement is experimentally increased, probably because of an increased rate of infanticide, but infanticides were not directly observed (Andreassen and Gundersen 2006, Opperbeck et al. 2012). Studies on bears and lions have suggested that the hunting of reproductive males could affect the dynamics of whole populations due to the increased rate in infanticide (Swenson et al. 1997, Whitman et al. 2004, Loveridge et al. 2010). However, there is still only scarce evidence from unmanipulated populations that infanticide matters at the population-level, and further studies are required to consolidate our understanding of the contribution of infanticide to population dynamics.

Infanticides occur mainly in species which can breed year-round and where reproduction is monopolized by a few males (Lukas and Huchard 2014), and a number of equids such as feral horses *Equus ferus*, Przewalski's horses *Equus ferus przewalskii*, mountain zebras *Equus zebra*, and plains zebras *Equus quagga*, display such characteristics. These species form harems where a

stallion (i.e. harem-male) is associated with several females and their dependent young, and can breed year round, traits that should have facilitated the evolution of infanticide. Males that do not hold a harem form loose bachelor groups and will eventually attempt to start a harem by 'abducting' young females, monopolizing dispersing young females or taking over a harem by replacing the stallion. In these harem-forming equids, infanticide by males is expected for several reasons (see references in Bartoš, Bartošová, & Pluháček, 2019; Ebensperger, 1998; Palombit, 2015). First, infanticide can reduce the latency for the next breeding attempt of the female. For instance, in plains zebras, the latency after a birth for the next breeding attempt can be as short as a few weeks and as long as 15 months (Barnier et al. 2012). If the costs of raising a foal influence the latency, then infanticide could potentially increase the stallion's reproductive success. Secondly, infanticide by stopping lactation can improve the body condition of the mother, thus increasing the chance that the pregnancy will be successful and the next foal will grow well. Finally, foals can be accidentally involved in fights and injured or killed, since newly established stallions usually exhibit high testosterone levels which, combined with the fact that mares may reject their mating attempts, can make for situations where the survival of foals is at risk.

Male infanticide following a stallion turnover (i.e. replacement of a stallion by a different male) has often been reported in equids, but mostly in small and domestic, captive or reintroduced populations (Camargue horses: Duncan, 1982; Przewalski's horses: Chen, Weng, Chao, Hu, & Taya, 2008; Dorj & Namkhair, 2013; Feh & Munkhtuya, 2008; Kolter & Zimmermann, 1988; Ryder & Massena, 1988). In captive plains zebras, 10 records of infanticidal attacks by males have been reported over 27 years of monitoring (Pluháček and Bartoš 2000, 2005, Pluháček et al. 2006). These are all populations where natural sociality had been disrupted. Infanticide could also be common in captive and recently reintroduced equids not because it is adaptive, but because the behaviour results from increased aggressiveness due to social stress (C. Feh, pers.comm.). Penzhorn (1985) reported indirect evidence for infanticide in wild mountain zebras, but observations of infanticide in wild equids are scarce: Gray (2009) observed an attempt of infanticide by a mustang, but argued that it was exceptional. Infanticide has been seen only once in wild plains zebras (Ransom and Kaczensky 2016) but the relationships of the foal to the harem in which it occurred are unknown. Forced copulations following stallion turnovers occurred regularly in the mustangs studied by Berger (1983), leading him to suggest that feticide – the abortion of a fetus due to forced mating or sexual harassment by a conspecific adult male - might be adaptive in horses and other equids. The importance of such behaviour in equids remains controversial however (Kirkpatrick and Turner 1991). Overall, the current state of knowledge is

unclear about whether infanticide is common or rare in equids, and whether it matters or not for the dynamics of their populations (as implicitly suggested in Grange et al., 2004).

Here we use a long term study of the behaviour and demography of a large wild population of plains zebras conducted since 2004 in Hwange National Park (HNP, Zimbabwe) where stallion turnovers were recorded and accurate data on pregnancy were obtained by hormone assays. This study offers a rare occasion to test for the occurrence of infanticide after stallion turnovers and assess the potential influence of these turnovers on foal survival in a wild equid.

Specifically, we test here the predictions that (1) the rate of stallion turnover increases with the number of reproductive females (i.e. subadult and adult females) in a harem, and (2) that foals in harems that experience, either as fetuses or soon after their birth, a stallion turnover have a lower survival probability than foals in harems where such event did not occur.

MATERIAL AND METHODS

Study species and site

The study was conducted in the eastern section of HNP in Western Zimbabwe over an area covering ca. 2000 km² (19°00'S, 26°30'E). The vegetation is dominantly bushy, characteristic of semiarid dystrophic savannas, but interspersed with patches of open grasslands (Chamaille-Jammes et al. 2006). The annual rainfall averages 600 mm, with most rains falling between November and April, the rainy season (Chamaille-Jammes et al. 2006). Predation pressure is high as lions *Panthera leo* are abundant (i.e. around 3.5 individuals 100 km⁻²) (Loveridge et al. 2016), and leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, and spotted hyenas *Crocuta crocuta* are also present, all known to attack zebra foals. In the study area, plains zebra density fluctuated slightly around 1 individual km⁻² (Chamaillé-Jammes et al. 2009b, Grange et al. 2015) between 2004 and 2017, when we monitored the behaviour and fate of individual zebras.

Plains zebra populations are made of two basic social units: harem and bachelor groups (Klingel 1969b, Estes and Otte 2012). Non-territorial harems are composed of a stallion and most often several adult females, subadults of both sexes, and dependent offspring. Subadult and adult females are hereafter referred to as 'reproductive females'. In the study area, harem sizes range between 2 and 10 individuals (median: 5 individuals), and are positively correlated to the number of reproductive females in harems (Spearman rank correlation: $r_s = 0.89$, $N = 51$, $P < 0.001$). Males that are not stallions form all-male bachelor groups, which range between 1 and 19 individuals

(median: 3 individuals), and sometimes attempt to take over a stallion's position. In harems, young males and females disperse when they are around 2 years old (y.o.): dispersing females join already existing harems or form a new group with a bachelor, and males join bachelor groups. Reproductive females may also change group, but this is rare: in this study, 92% of mares (N = 453) were still in the same harem after one year and 86% (N = 342) after two years.

Data collection

Observations were made twice a year, approximately one month in the wet season (between February and April) and three weeks in the dry season (between July and September). These monitoring periods are hereafter referred to as 'sessions'. We focused on harems, and determined group composition and identified new individuals. The zebras were identified by their unique stripe patterns (Grange et al. 2015) and were categorized into four age-classes: foal, from birth to 1 y.o.; yearling, between 1 and 2 y.o.; subadult, between 2 and 4 y.o.; and adults, 4 y.o. and older. The age of previously unobserved young individuals was estimated using Penzhorn's criteria (Penzhorn 1982) combined with photos of foals of known age in the Hwange population. We used suckling behaviour as criteria to determine motherhood (as in Barnier et al., 2012). Indeed, although the possibility for adoption and allosuckling cannot be fully discarded, these events are very rare in equids (Pluháček et al. 2010, Olléová et al. 2012, Topczewska et al. 2018). In addition, we opportunistically collected dung samples from females (N = 357 from 90 mares); these were air-dried within 48h after collection and stored at room temperature until analysis for immunoreactive 20-oxopregnane and estrogen metabolite concentrations (Ncube et al. 2011, Barnier et al. 2012). Hormone concentrations allowed females to be allocated to non-pregnant, mid-pregnancy (9 to 3 months to foaling) or late pregnancy (3 to 0 months to foaling) stages (Ncube et al. 2011). Thanks to this information, we knew that a foal had been born even when it died before we resighted the harem, or had been lost by abortion. We could therefore compare the survival probability of foals in their first year in harems with or without a stallion turnover, assuming that if the mother is observed, the detection probability of the foal if it is alive is 1. Under this realistic assumption, the observation of a mare, previously detected pregnant, without her foal is reliable evidence that the foal had not survived, as foals are dependent on their mother until the age of about 1 year. More details about the demographic monitoring of this population can be found in Grange et al. (2015). Demographic data and data on hormone levels collected between 2008 and 2017 are used here, corresponding to 19 sessions (10 in the wet season and 9 in the dry season) over 10 years.

During these sessions, ad hoc observations of behaviour were made, including attacks, mating and foaling. Although we did not specifically keep track of observation time, we estimated that a minimum of 5400 hours were spent directly observing zebras between July 2004 when the study started, and the last session in October 2019.

Data analysis

We first tested whether the probability of stallion turnover increases with the number of reproductive females in a harem (analysis 1). Stallion turnover was considered to have occurred if a harem was seen during two consecutive sessions with a different stallion at each session. For this analysis, we did not use information when the resighting of a harem occurs more than a year later (i.e. when the harem was not seen in two consecutive sessions), as there was too much uncertainty about how the number of reproductive females had changed during this period. In total, we observed 30 turnovers, out of 232 possible occasions where it could have occurred (i.e. when a harem is seen during a session and reobserved within a year, regardless of the stallion identity). We fitted generalized linear mixed models with logit links and a binomial distribution for errors to test the relationship between the likelihood of having observed a stallion turnover (response variable, binary coded with 1 for turnover and 0 for no turnover) and the number of reproductive females in the harem at the first session. To account for the fact that turnovers are more likely to occur as time passes, we included an additive effect of the log-transformed number of days between the two sessions. We also included the identity of the stallion and the identity of the harem as random effects on the intercept to account for the fact that stallions and harem females could differ in their ability to repel (for stallions) or willingness to accept (for females) an external male.

We also investigated whether stallion turnover affected the survival probability of foals (analysis 2), using the data obtained from the hormone analyses conducted on the dung samples. We focused on mares detected pregnant through hormone analyses (N = 29 in late pregnancy and N = 71 in mid-pregnancy) and compared the probability of reobserving them with a foal at the next session when the stallion was replaced between the date of dung sampling and the date of the first resighting of the mare at the next session, and when a stallion turnover did not occur. Females detected in mid-pregnancy are between 9 and 3 months to the foaling date, so observing them without a foal at the next session could indicate that the foal had been aborted or died, but it is also possible that the foal was not yet born. However, this possible bias is independent of whether or not a stallion turnover occurred and will therefore not affect our results. Focusing only on females detected in mid-pregnancy (N = 89), we also tested the effect of stallion turnover on

the probability of seeing a foal two sessions later (rather than at the next session). As the duration over which survival was estimated was greater, this analysis was more likely to be affected by other sources of mortality, and we consider it less robust, but note that it provided qualitatively similar results (Appendix: Tables S1-S2, Fig. S1). We sometimes obtained two dung samples in the same pregnancy (N = 25), and if we did and the female was in late pregnancy it has been included in the analysis of late-pregnant females. In all cases the second sample also identified the female as pregnant (i.e. no abortion was observed). We tested the effect of stallion turnover on the probability of observing a foal at the next session (coded 1 = mare re-observed with a foal, 0 = mare re-observed without a foal) by fitting generalized linear mixed models with logit links and binomial distributions for errors. Explanatory variables included: a binary variable coding for whether stallion turnover had occurred; the log-transformed number of days between the date of dung sampling and the date of first resighting of the mare, to control for the expected effect of the time between the date of dung sampling and the date of first resighting of the mare on foal survival; age of the mare, to account for its many potential positive effects on pregnancy success (e.g. Bartoš, Bartošová, & Pluháček, 2015; Bartoš, Bartošová, Pluháček, & Šindelářová, 2011) and foal survival (e.g. Cameron, Linklater, Stafford, & Minot, 2000); and season, to account for the potential influence of seasonal changes in forage quality and possibly predation risk, with the hypothesis that foal survival should be lower in the dry season: forage quality is lower, zebras remain near the few remaining waterholes that are also focus areas for hunting lions, and zebras' strategy to reduce this risk might be costly (see Courbin et al., 2019). We also included the identity of the mare as a random effect nested within a harem identity random effect, as we had repeated measures on the same individuals.

For both analyses 1 and 2, we first fitted and reported full models, i.e. models integrating the explanatory variables presented above. Models were fitted in a Bayesian framework using Stan (Carpenter et al. 2017) accessed using the *brms* package (Bürkner 2017) in R (R Core Team 2019). We used the non-informative default priors, and for each model ran four chains with 4000 iterations each and checked for convergence and quality of fit using the recommended criteria (visual inspection of trace plot, $R_{hat} < 1$, effective sample size $> 0.5 * \text{post-warmup samples}$, posterior predictive checks) (Conn et al. 2018). We based our assessment of the strength of the relationship between explanatory variables and response variables on the model coefficients and their 95% credible intervals. We also compared the predictive accuracy of models with and without the explanatory variable of interest. We did so using the leave-one-out information criterion (LOO-IC), a cross validation approach recommended by Vehtari, Gelman, & Gabry (2017)

for Bayesian models. Smaller LOO-IC values indicate better predictive models, and LOO-IC differences can be obtained with associated standard errors (SE) (Vehtari et al. 2017).

RESULTS

The average probability of a stallion turnover between two sessions increases with the number of reproductive females in harems (Table 1), varying from 0.03 to 0.43 for harems which have from 1 to 5 reproductive females (Fig. 1). Removing the number of reproductive females from the models clearly reduced their out-of-sample predictive ability (Appendix: Table S3; in particular, note that $\text{LOO-IC}(\text{model 3, best model without the number of reproductive females}) - \text{LOO-IC}(\text{model 1, best model with the number of reproductive females}) = 14.94 \pm 7.94 \text{ SE}$).

Table 1. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability of stallion turnover between two sessions ($\text{Pr}_{(\text{turnover})}$). Variables are: the number of reproductive females (N_{fem}) and the log-transformed number of days between the two sessions ($\log(\text{Days})$) as fixed effects, and identities of the stallion ($\text{ID}(\text{Stallion})$) and of the harem ($\text{ID}(\text{Harem})$) as random effects. The estimates and their 95% credible intervals (95% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI
Group-level ('random') effects	ID(Stallion)	1.60	0.39 – 3.19
	ID(Harem)	0.55	0.02 – 1.57
Population-level ('fixed') effects	Intercept	-15.15	-25.00 – -7.21
	N_{fem}	1.25	0.60 – 2.05
	$\log(\text{Days})$	1.79	0.43 – 3.38

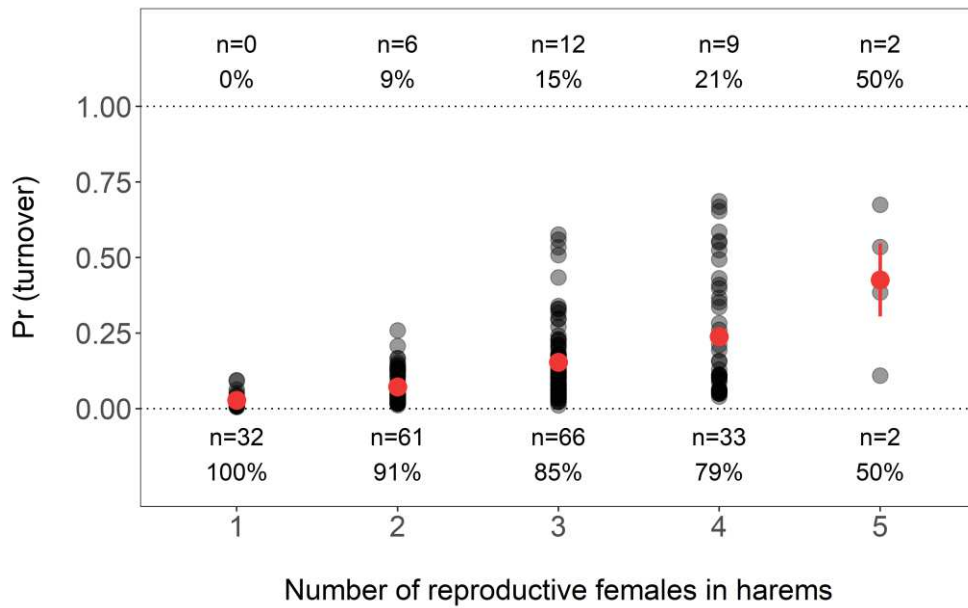


Figure 1. The probability of a stallion turnover between two consecutive sessions as a function of the number of reproductive females in the harems at the first session. The black dots show the predictions from the model, for all observations of the dataset, with the mean \pm SE of these values shown in red. For each category of the number of reproductive females, we also report the sample size (also expressed as percentage of observation for the category) of turnover (1) or no turnover (0).

Over the >5400 hours of monitoring, we never witnessed an infanticide, or even a stallion attacking a foal. Such behaviour was also never reported to us by other researchers or tourist guides working in the area. The probability of observing a foal at the next session did not differ between situations when a stallion turnover occurred and those when it did not (Table 2, Fig. 2). Models with stallion turnover as predictor had lower out-of-sample predictive ability than many models without (Appendix: Table S4; in particular, note that $\text{LOO-IC}(\text{model 6, best model with stallion turnover}) - \text{LOO-IC}(\text{model 1, best model without stallion turnover}) = 2.76 \pm 4.08 \text{ SE}$).

Table 2. Coefficients of the mixed model investigating the effect of stallion turnover on the probability of observing a foal at the next session ($Pr_{(obs\ next\ session)}$). Variables are: stallion turnover (Turnover, binary: no turnover (false), turnover (true)), the log-transformed number of days between the date of dung sampling and the date of first resighting of the mare (log(Days)), age of the mare in months when first resighted (Age(mare)), and season (Season, dry, wet) as fixed effects; and identities of the mare (ID(Mare)) and the harem (ID(Harem)) as nested random effects. The estimates and their 95% credible intervals (95% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI
Group-level ('random') effects	ID(Harem)	0.88	0.04 – 2.24
	ID(Harem):ID(Mare)	0.95	0.04 – 2.62
Population-level ('fixed') effects	Intercept	3.49	-10.00 – 17.07
	Turnover_true	-0.41	-1.95 – 1.12
	log(Days)	-1.26	-4.06 – 1.39
	Age(mare)	0.02	0.00 – 0.04
	Season_wet	1.18	0.03 – 2.44

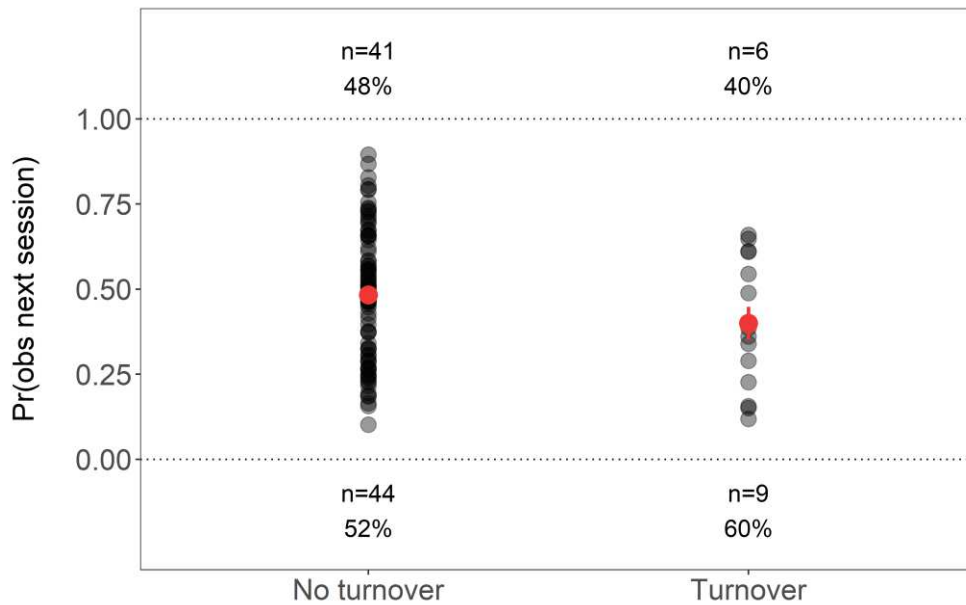


Figure 2. The probability of observing a foal at the next session in relation to whether or not the stallion was replaced in the meantime. The black dots show the predictions from the model, for all observations of the dataset, with the mean \pm SE of these values shown in red. For each category of stallion turnover, we also report the sample size (also expressed as percentage of observation for the category) of foal observed (1) or not observed (0) at the next session.

The analysis of data from females observed mid-pregnant and resighted two sessions later also supported a lack of relationship between the probability of foal survival and whether or not the stallion was replaced between the two sessions (Appendix: Tables S1-S2). We note however that the estimated survival difference was greater, with a tendency for survival to be lower when stallion had changed (Appendix: Fig. S1).

DISCUSSION

This study shows that the frequency of stallion turnover increases with increasing number of reproductive females in harems, therefore supporting our prediction. More importantly, there is however no significant reduction in foal survival after a takeover. This result strongly suggests that infanticides by males do not occur in this wild population of plains zebras, or are so rare that infanticide has negligible effects on foal survival at the population level. We therefore question the common - but poorly supported - idea that plains zebras are a case of sexually selected infanticide by males. Our results highlight the weak effect of social factors in regulating plains zebra population.

Higher rate of stallion turnovers in larger female groups

As predicted, the frequency of stallion turnovers increases with the number of reproductive females in a harem. Similar results have been found in other species, mainly in non-human primates (red howlers: Crockett & Janson, 2000; colobus monkeys: Teichroeb et al. 2012; Thomas's langurs: Steenbeek & Van Schaik, 2001; geladas: Dunbar 1984). To our knowledge, this is the first demonstration that this effect of group size holds in equids. Larger groups may be more attractive for bachelor males, the presence of many females increasing their chance of siring their own offspring following harem takeover. However, females are not passive resources and their choice, although not well understood yet, may be important in accepting a new stallion and in shaping the benefits gained by the incoming male in terms of reproductive success (Smuts and Smuts 1993). For instance, there are some observations of female wild horses that managed to prevent forced copulations by kicking and escaping from the newly established male (Berger 1986). Another possibility to explain the positive relationship between rate of male turnover and female group size is that larger harems with many females may be more difficult for the stallion to defend against intruding males, therefore increasing the likelihood of being taken over by a bachelor male. For instance, in wild horses, the energy invested by stallions in the defense of their harems increases with harem size, but the energy cost per female defended was reduced in larger harems, which could make them more attractive to bachelors (Berger 1986). Finally, harems composed of many reproductive females provide a more heterogeneous mating opportunity for the incoming male, the more numerous these females are, the greater the chance that some of them are not pregnant and available for reproduction.

In conclusion to this section, harem takeovers are frequent in this population, and larger females groups are more likely to experience stallion turnovers.

Lack of evidence for male infanticide or forced matings following harem takeover

In captive plains zebras, forced copulations and attacks on foals have been observed (Pluháček and Bartoš 2005, Pluháček et al. 2006). However, in this wild plains zebra population, no forced mating or infanticide event, nor even an attack of a stallion towards a foal, has been seen in more than 15 years of observations, with over 5400 hours spent watching the animals. This suggests that infanticide, if it occurs, is extremely rare. It also suggests that the lack of significant effect of stallion turnovers on foal survival is unlikely to be the result of a 'masking' of infanticide by high foal mortality induced by predation. We acknowledge that some may consider that there might be a trend towards poorer survival after a takeover when longer time scale is considered (Appendix: Fig. S1), but if this is confirmed in the future, it could of course result from many other

causes than infanticide. Young foals are weak and they often make inappropriate responses, and may get killed by accident, in situations where stallions and other individuals are involved in attacks and chases as often happens during takeovers. This has been reported in horses for instance (C. Feh & P. Duncan, pers. obs.; Duncan, 1992). Further, the new male may be less attentive to protecting foals from predators. Based on much more limited data, Klingel (1967) found a similar result in the Tanzania's Ngorongoro Crater population, where no infanticide was observed, although several takeovers of harems composed of pregnant females and young foals were recorded. Jaworska et al. (2020) reported similar findings in a population of semi-feral Konik polski horses *Equus caballus* where, over 31 years of monitoring, infanticide by males was never observed and stallion turnovers had no significant effects on female reproductive success. These results contrast with studies of other harem-forming species where male infanticide following harem-male turnovers has been found (e.g. in lions: Bertram, 1975; Packer et al., 1988; Packer & Pusey, 1983; blue monkeys: Butynski, 1982, 1990). In wild horses, female reproductive success to the next parturition season was significantly lower in unstable groups that experienced a stallion turnover compared to stable groups (Berger 1986), and, in reintroduced Przewalski's horses, 9% of all foal mortality reported was attributed to infanticide by a newly established stallion (53 of 580 foals between 1994 and 2019) (Dorj & Namkhai, 2013; U. Dorj, pers.comm.).

Although our results do not provide evidence for infanticide in wild plains zebra, this behaviour has been observed for this species in captivity and the social and mating system of plain zebras should favor the emergence of infanticide behaviour (Lukas and Huchard 2014). In captive plains zebras, Pluháček & Bartoš (2005) found that foal killing is common (when the stallion changed, the probability of foal to die was almost 100% for foals less than two months old). This raises the question of why the situation is so different in the wild: a possible explanation is that conditions in captivity and recent reintroduction may alter the behaviour of the animals and elevate the frequency of infanticide events, the 'social pathology hypothesis' (discussed by Feh & Munkhtuya, 2008; Van Schaik & Janson, 2000).

To account for the lack (i.e. or rarity) of infanticide in our wild population of plains zebras although the species presents traits that should favour this behaviour, we see several possible hypotheses: (1) the killing of a dependent offspring benefits infanticidal males only if it improves their reproductive success by shortening the interbirth interval of the mother, and this may not be the case in plains zebras. In Przewalski's horses, Feh & Munkhtuya (2008) found that infanticide did not reduce interbirth intervals and that mares whose foals had been attacked avoided affiliating with the infanticidal male later on, therefore contesting the 'sexual selection hypothesis' and calling into question the necessity for the incoming male to kill a dependent

young in such condition. However, infanticide may still improve the reproductive success of infanticidal males by stopping lactation and improving the mare's body condition and subsequent pregnancy success. Despite this potential benefit, males do not appear to commit infanticide. This is unexpected, especially at a site like Hwange where a male's reproductive period may be limited by both high intra-male competition and high predation risk, as we would expect any possibility increasing their chance to reproduce to be used by males. Therefore, either these purported benefits do not exist, or, we tentatively suggest, it could be that the high foal losses due to predation reduce the need for males to resort to infanticide; (2) female plains zebras may have developed counterstrategies such as female sociality and/or maternal aggression and protectiveness, allowing them to protect their progeny against intruders. For instance, in feral horses, higher maternal protection when several males are present in a group and higher protection towards foals that are not sired by the stallion have been reported (Cameron et al. 2003, Gray 2009, Watts et al. 2020). In captive mountain zebra, a female was observed to actively defend her foal against an infanticidal male (Joubert 1972), and similarly, in Przewalski's horses, all females whose foal was attacked by an infanticidal male strongly defended their foal, and in one case, the mare was helped by her half-sister (Feh and Munkhtuya 2008). In wild horses, females have been shown to cooperate and help each other at aggressively repelling newly established males that coerce females to mate following group takeover (Berger 1986). These strategies are likely to exist in plains zebra too, although it has never been documented in this species; (3) the low level of sexual dimorphism in plains zebra may deter infanticidal males from attacking foals: as females and males have similar body sizes, attempts at male infanticide could lead to severe injuries by the mother.

CONCLUSION

In conclusion, this study offers the first demonstration for an equid that male turnover rates are high in the wild, and increase with female group size. Based on work in captivity, this species is commonly cited as an example of species in which male infanticide occurs. However, our results reveal a lack of evidence for infanticide by males in the wild for this species, and if it occurs at all, it could have only negligible effects on foal survival at the population level, which is a key factor underlying the dynamics of this population (Grange et al. 2015). More generally, our study shows that demographic signals of *a priori* important social processes should be investigated closely rather than assumed.

ACKNOWLEDGMENTS

We thank the Director General of the Zimbabwe Parks and Wildlife Management Authority for providing the opportunity to carry out this research. We acknowledge the support of the 'Zone Atelier' program of the CNRS. We also thank the many people – too numerous to be named here - involved in this project over the years. We are particularly grateful to Claudia Feh for discussions on the conceptual framework which were more than useful. This work was supported by the French 'Agence Nationale de la Recherche' (grants SAVARID ANR-11-CEPS-003 and LANDTHIRST ANR-16-CE02-0001-01) and a PhD fellowship from 'Université de Montpellier' to C.V.

APPENDIX

Effect of stallion turnovers on the probability of observing a foal two sessions later

Focusing on females detected in mid-pregnancy ($N = 89$), we investigated the effect of stallion turnovers on the probability of re-observing these mares with a foal two sessions later (rather than at the next session) when the stallion was replaced between the date of dung sampling and the date of the first resighting of the mare two sessions later, and when a stallion turnover had not occurred. The probability of observing a foal two sessions later did not differ significantly between situations when a stallion turnover occurred and those when it did not (Table S1, Fig. S1). The best predictive model that include stallion turnover as a predictor (model 1) did not have a better predictive power than the null model (model 2) ($\Delta\text{LOO-IC}$ between model 1 and 2 is 0.50 ± 4.22 SE) (Table S2).

Table S1. Coefficients of the mixed model investigating the effect of stallion turnover on the probability of observing a foal two sessions later ($\text{Pr}_{(\text{obs two sessions later})}$). Variables are: stallion turnover (Turnover, binary: no turnover (false), turnover (true)), the log-transformed number of days between the date of dung sampling and the date of first resighting of the mare ($\log(\text{Days})$), age of the mare in months when first resighted ($\text{Age}(\text{mare})$), and season (Season, dry, wet) as fixed effects; and identities of the mare ($\text{ID}(\text{Mare})$) and the harem ($\text{ID}(\text{Harem})$) as nested random effects. The estimates and their 95% credible intervals (95% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI
Group-level ('random') effects	ID(Harem)	1.02	0.05 – 2.50
	ID(Harem):ID(Mare)	0.93	0.04 – 2.49
Population-level ('fixed') effects	Intercept	-14.49	-61.99 – 30.24
	Turnover_true	-1.15	-2.84 – 0.31
	$\log(\text{Days})$	2.21	-5.40 – 10.18
	Age(mare)	0.01	-0.01 – 0.04
	Season_wet	-0.72	-1.93 – 0.41

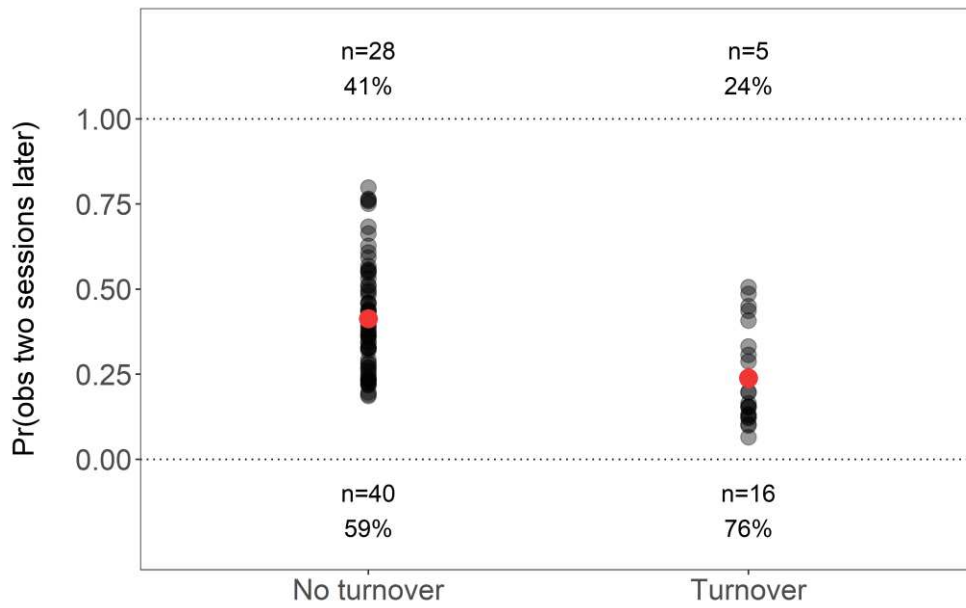


Figure S1. The probability of observing a foal two sessions later in relation to whether or not the stallion was replaced in the meantime. The black dots show the predictions from the model, for all observations of the dataset, with the mean \pm SE of these values shown in red. For each category of stallion turnover, we also report the sample size (also expressed as percentage of observation for the category) of foal observed (1) or not observed (0) two sessions later.

Table S2. Statistics of models investigating the effect of stallion turnover on the probability of observing a foal two sessions later ($\text{Pr}_{(\text{obs two sessions later})}$). Models could include the effects of stallion turnover (*turnover*), the log-transformed number of days between the date of dung sampling and the date of first resighting of the mare ($\log(\text{Days})$), age of the mare when first resighted ($\text{Age}(\text{mare})$), and season (*ss*) as fixed effects; and identities of the mare ($\text{ID}(\text{Mare})$) and the harem ($\text{ID}(\text{Harem})$) as nested random effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. Leave-one-out cross-validation information criterion (LOO-IC) and standard errors (SE) are shown.

Models	Model ID	LOO-IC	SE
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \#$	1	122.2	7.7
$\text{Pr}_{(\text{obs two sessions later})} \sim 1 + \#$	2	122.7	6.3
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{Age}(\text{mare}) + \#$	3	122.7	7.1
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{ss} + \#$	4	122.9	7.3
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \text{Age}(\text{mare}) + \#$	5	123.4	8.2
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \text{ss} + \#$	6	123.9	8.7
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{Age}(\text{mare}) + \text{ss} + \#$	7	124.3	8.2
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \log(\text{Days}) + \#$	8	124.4	8.1
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \text{Age}(\text{mare}) + \text{ss} + \#$	9	125.0	9.3
$\text{Pr}_{(\text{obs two sessions later})} \sim \log(\text{Days}) + \#$	10	125.2	6.8
$\text{Pr}_{(\text{obs two sessions later})} \sim \log(\text{Days}) + \text{Age}(\text{mare}) + \#$	11	125.9	7.5
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \log(\text{Days}) + \text{Age}(\text{mare}) + \#$	12	125.9	8.6
$\text{Pr}_{(\text{obs two sessions later})} \sim \log(\text{Days}) + \text{ss} + \#$	13	126.0	7.9
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \log(\text{Days}) + \text{ss} + \#$	14	126.3	9.2
$\text{Pr}_{(\text{obs two sessions later})} \sim \log(\text{Days}) + \text{Age}(\text{mare}) + \text{ss} + \#$	15	126.6	8.6
$\text{Pr}_{(\text{obs two sessions later})} \sim \text{turnover} + \log(\text{Days}) + \text{Age}(\text{mare}) + \text{ss} + \#$	16	128.2	10.0

$\#(1|\text{ID}(\text{Harem})/\text{ID}(\text{Mare}))$

Effect of the number of reproductive females in harems on the probability of stallion turnover

Table S3. Statistics of models investigating the effect of the number of reproductive females in harems on the probability of stallion turnover between two sessions ($\text{Pr}_{(\text{turnover})}$). Models could include the effects of the number of reproductive females (N_{fem}) and the log-transformed number of days between the two sessions ($\log(\text{Days})$) as fixed effects; and identities of the stallion ($ID(\text{Stallion})$) and the harem ($ID(\text{Harem})$) as random effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. Leave-one-out cross-validation information criterion (LOO-IC) and standard errors (SE) are shown.

Models	Model ID	LOO-IC	SE
$\text{Pr}_{(\text{turnover})} \sim N_{fem} + \log(\text{Days}) + \#$	1	155.2	19.9
$\text{Pr}_{(\text{turnover})} \sim N_{fem} + \#$	2	161.1	20.3
$\text{Pr}_{(\text{turnover})} \sim \log(\text{Days}) + \#$	3	170.2	20.4
$\text{Pr}_{(\text{turnover})} \sim 1 + \#$	4	173.0	20.1

$\# (1 | ID(\text{Stallion})) + (1 | ID(\text{Harem}))$

Effect of stallion turnover on the probability of observing a foal at the next session

Table S4. Statistics of models investigating the effect of stallion turnover on the probability of observing a foal at the next session ($Pr_{(obs\ next\ session)}$). Models could include the effects of stallion turnover (*turnover*), the log-transformed number of days between the date of dung sampling and the date of first resighting of the mare ($log(Days)$), age of the mare when first resighted ($Age(mare)$), and season (*ss*) as fixed effects; and identities of the mare ($ID(Mare)$) and the harem ($ID(Harem)$) as nested random effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. Leave-one-out cross-validation information criterion (LOO-IC) and standard errors (SE) are shown.

Models	Model ID	LOO-IC	SE
$Pr_{(obs\ next\ session)} \sim Age(mare) + ss + \#$	1	139.0	7.5
$Pr_{(obs\ next\ session)} \sim Age(mare) + \#$	2	139.1	6.4
$Pr_{(obs\ next\ session)} \sim 1 + \#$	3	140.3	4.9
$Pr_{(obs\ next\ session)} \sim ss + \#$	4	140.5	6.1
$Pr_{(obs\ next\ session)} \sim log(Days) + Age(mare) + ss + \#$	5	141.1	7.9
$Pr_{(obs\ next\ session)} \sim turnover + Age(mare) + \#$	6	141.8	6.9
$Pr_{(obs\ next\ session)} \sim turnover + Age(mare) + ss + \#$	7	141.8	8.0
$Pr_{(obs\ next\ session)} \sim log(Days) + ss + \#$	8	142.0	6.5
$Pr_{(obs\ next\ session)} \sim log(Days) + Age(mare) + \#$	9	142.1	6.8
$Pr_{(obs\ next\ session)} \sim log(Days) + \#$	10	143.2	5.1
$Pr_{(obs\ next\ session)} \sim turnover + \#$	11	143.2	5.2
$Pr_{(obs\ next\ session)} \sim turnover + ss + \#$	12	143.2	6.5
$Pr_{(obs\ next\ session)} \sim turnover + log(Days) + Age(mare) + ss + \#$	13	143.8	8.5
$Pr_{(obs\ next\ session)} \sim turnover + log(Days) + Age(mare) + \#$	14	145.0	7.2
$Pr_{(obs\ next\ session)} \sim turnover + log(Days) + \#$	15	145.8	5.6
$Pr_{(obs\ next\ session)} \sim turnover + log(Days) + ss + \#$	16	146.1	7.2

(1|ID(Harem)/ID(Mare))

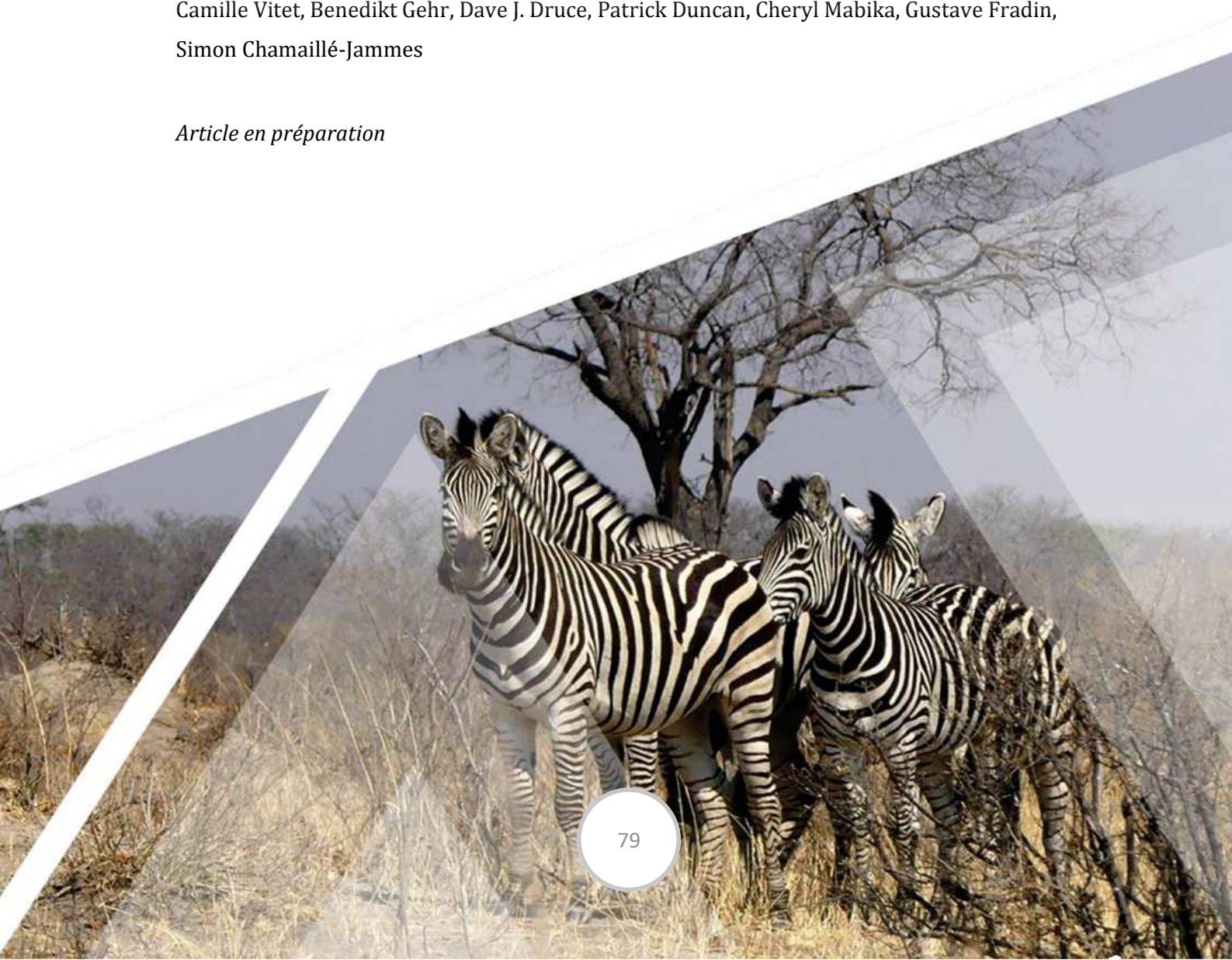
CHAPITRE 3

Vegetation cover facilitates the avoidance of bachelors by larger harems in plains zebras, with consequences for stallion turnovers

Le couvert végétal facilite l'évitement des *bachelors* par les grands harems chez le zèbre des plaines, avec des conséquences sur les changements d'étalon au sein des harems

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Article en préparation



ABSTRACT

In multilevel societies of plains zebras *Equus quagga*, harems (i.e. single-male family groups) and bachelor groups (i.e. all-male groups) frequently aggregate into larger unstable herds, and harems have been found to herd with other harems in response to an increase probability of encountering bachelors (Rubenstein and Hack 2004). Group size and habitat structure are factors that may shape associations of groups: (i) larger harems with many reproductive females may seek to herd with other harems and to avoid bachelors as they are potentially more likely to be targeted by bachelors that are looking to secure mating opportunities, and (ii) open habitats may facilitate herd formations and/or prevent groups to avoid each other. Here, we use demographic data collected in two natural populations of plains zebras in Hwange National Park (HNP, Zimbabwe) and Hluhluwe-iMfolozi Park (HiP, South Africa) where composition of herds and stallions turnovers were recorded. We tested the predictions that larger harems with many reproductive females are (i) more likely to be observed alone than smaller harems, as they are supposed to benefit from a reduced predation risk, and (ii) more likely to be observed in herd with other harems and less likely to be observed in herd with at least one bachelor group than harems with fewer reproductive females, due to the higher threat bachelors represent for them. Results show that the number of reproductive females in harems has no effect on the probability for harems to be alone or with other harems, whereas harems with more reproductive females seems to be found less often near bachelors (although significant uncertainty remains). We also found that associations of groups are more common in open vegetation, especially harem-bachelors associations for which largely open areas clearly make associations more likely. This suggests that harems including many reproductive females may seek to avoid bachelors, and actually seem to have more success in doing it in HiP where vegetation is overall more closed than in HNP. In accordance with this, we tested the prediction that, in HiP, the probability of stallion turnovers does not increase with increasing number of reproductive females in harems (unlike what was found in HNP, Vitet et al. submitted) and results supported our prediction. Overall, this study suggests that the number of reproductive females in harems and vegetation cover both influence associations of plains zebra groups, especially harems-bachelors associations, therefore expanding our vision of the drivers of spatial associations between groups within populations.

KEYWORDS: equids, group size, habitat structure, herd formation, male turnover, multilevel society

INTRODUCTION

Multilevel societies are among the most complex social systems that exist in the animal kingdom (Clutton-Brock 2016, Ward and Webster 2016, Grueter et al. 2017b). In these societies, individuals are part of socially stable core units that move through the environment and frequently aggregate with one another in higher hierarchical tiers, forming herds that vary in size and composition over time and can reach several hundred individuals (Grueter et al. 2017b). Multilevel societies differ from other forms of fission-fusion social systems in the sense that herds, when separating, split into their social subunits that are generally socially cohesive and sometimes clearly spatially delimited (Grueter et al. 2012), while in fission-fusion systems, herds split in subgroups of variable size, composition, and cohesiveness (Aureli et al. 2008).

Several explanations have been proposed to explain the formation of higher tiers in these societies. Associating temporarily with other groups can provide benefits to face specific environmental conditions, in space or time. For example, the formation of herds can provide a better protection against predators (Rubenstein 1986, Schreier and Swedell 2009, Tong et al. 2015, Lin et al. 2020). Indeed, as group size increases, the presence of additional neighbours could dilute the risk for each individual of being predated during an attack, under the assumption that the predator can only take one prey at a time and that attack rate does not increase with prey group size (the dilution effect; Bertram 1978, Turner and Pitcher 1986, Lehtonen and Jaatinen 2016). Moreover, with increasing group size, the probability of detecting an approaching predator could increase as more individuals monitor the environment (the detection effect; Lima, 1995; Pulliam, 1973). The formation of herds can also supply shelters against difficult climatic conditions and provide thermoregulatory advantages (Nowzari et al. 2013). Finally, in species where bachelors (i.e. extra-group males) compete to get access to female groups, associating with other family groups can reduce the amount of harassment of females by bachelors, the risk of bachelors incursion into family groups and the risks of male turnover and infanticide through joint defence of males from these family groups (the bachelor threat hypothesis; Rubenstein 1986; Rubenstein and Hack 2004; Grueter and Van Schaik 2010; Pappano et al. 2012).

In most of these situations, group size can affect the propensity of groups to associate in herds with other groups. Some studies conducted on non-human primate species showed that larger groups with many reproductive females are more likely to be targeted by bachelors that are looking to secure mating opportunities (Dunbar 1984, Crockett and Janson 2000, Bergman et al. 2009) and are therefore more at risk of male turnovers and infanticides. This social pressure incurs by larger groups with many reproductive females could encourage them to associate with

other family groups and to avoid bachelors. In the case of anti-predator behaviour, larger groups are expected to face a lower risk of predation than smaller groups due to the dilution effect (Bertram 1978, Turner and Pitcher 1986, Lehtonen and Jaatinen 2016) and the detection effect (Pulliam 1973, Lima 1995), and this could enhance the propensity of smaller groups to herd with other groups in order to dilute their risk of predation and benefit from a better detection of predators.

The habitat structure can also affect the probability of associations between groups. In the blackbuck antelope, Isvaran (2007) showed that associations between groups were facilitated in large stretches of open habitats. Open and weakly fragmented areas may be beneficial for groups that want to associate with other groups, as they may provide greater visibility and increase the possibility for individuals to perceive groups of conspecifics, therefore facilitating herd formations (Gerard et al. 1993). This hypothesis was supported by several studies that found a positive correlation between habitat openness and rate of herd formation (Gerard and Loisel 1995, Gerard et al. 2002, Pays et al. 2007a, Fortin et al. 2009). However, open habitats may be detrimental for groups that seek to isolate themselves, and in that case, closed habitats may provide opportunities for groups to avoid each other. Therefore, the probability for social core units to associate in higher tiers is likely to vary depending on the environmental conditions (e.g. habitat openness) and the sizes of groups and their associated ecological and social pressures (e.g. predation risk, bachelor threat).

Plains zebras could be an excellent model species to investigate the role of group size and environment in shaping social associations between groups. Plains zebras live in multilevel societies composed of only two tiers with two basic social units - harems (i.e. single-male family groups) and bachelor groups (i.e. all-male groups) - that frequently aggregate into larger unstable herds (Klingel 1967, 1969b, Rubenstein and Hack 2004, Estes and Otte 2012). Given the current state of knowledge, zebra stallions (i.e. harem-males) appear to show a higher propensity to band together (with their harems) to fend off bachelors as the probability of encountering bachelors increases (Rubenstein and Hack 2004). This strategy (i.e. associating with other harems and avoiding bachelor groups) could be particularly favoured by larger harems. Indeed, in the plains zebra population of Hwange National Park (Zimbabwe), the frequency of stallion turnovers increases as the number of reproductive females in harems increases (Vitet et al., submitted), suggesting that larger harems with many reproductive females incur a higher risk of male turnover than smaller ones. However, to the best of our knowledge, little is known about the role of group size and environment in shaping associations between social groups in multilevel societies.

Here, we use data from individual-based demographic monitoring programs of plains zebras conducted in two natural populations: in Hwange National Park (HNP, Zimbabwe) and Hluhluwe-iMfolozi Park (HiP, South Africa). These two study areas differ in terms of habitat structure: the landscape is more closed in HiP (Fig. 1A) than in HNP (Fig. 1B). In both populations, we tested the predictions that larger harems with many reproductive females are more likely to be observed alone or in herd with at least another harem (i.e. no bachelors in the herd), and are less likely to be observed in herd with at least one bachelor group than smaller harems with fewer reproductive females. As results supported this last hypothesis in the HiP population, we then tested the prediction that the frequency of stallion turnovers does not increase with increasing number of reproductive females in harems in that population, unlike what was found in the plains zebra population of HNP. Given that the landscape in HNP is composed of large and attractive patches of open grasslands, we also tested the prediction that harems of the HNP population are generally less likely to be observed alone and more likely to be observed in herd with at least another harem or at least one bachelor group than harems from the HiP population. Overall, this study offers to discover whether harem size, the openness of the environment, and possibly an interplay between both, influence the propensity of harems to associate in herd with other groups (harems and/or bachelor groups).

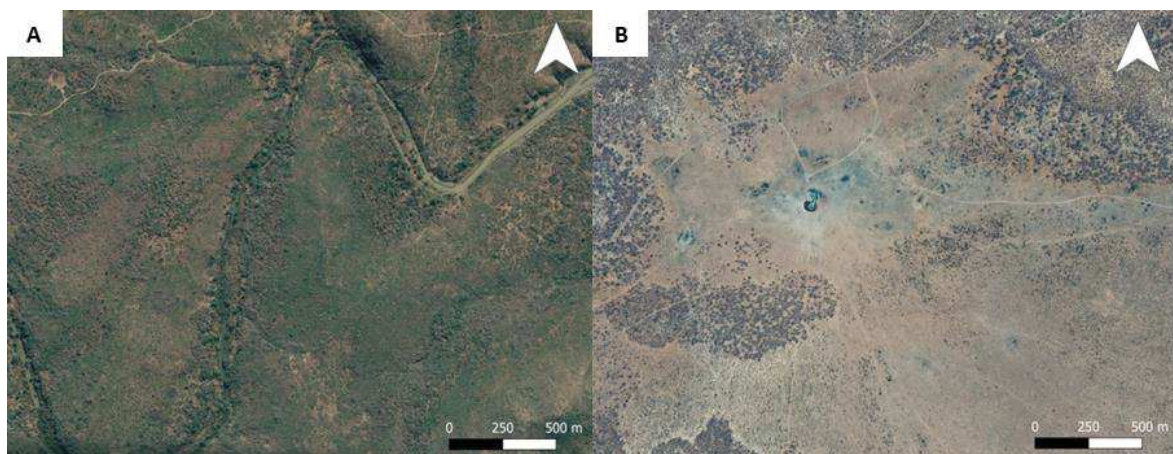


Figure 1. Satellites views of typical landscapes in Hluhluwe-iMfolozi Park (closed habitat) (A) and Hwange National Park (open habitat) (B) (source: Google Earth images).

MATERIAL AND METHODS

Study sites and species

Hluhluwe-iMfolozi Park is located in eastern South Africa, in the KwaZulu-Natal province (28°00'-28°26'S, 31°43'-32°09'E) over an area of c. 900 km². Vegetation in the park is diverse, ranging

from closed woodlands to grasslands (Howison et al. 2017). Grasslands represent 1.42 % of the landscape in HiP (Howison et al. 2017). Altitude and rainfall vary widely, decreasing from Hluhluwe (990 mm y⁻¹ and 750 m asl) to iMfolozi (635 mm y⁻¹ and 60 m asl) with most rains falling during the wet season between October and March (Howison et al. 2017). The park is virtually free of artificial water sources but there are several perennial rivers and, in the wet season, numerous ephemeral waterholes are found across the park. The density of plains zebras is estimated to fluctuate around 2 individuals km⁻² from 2010 until now (Le Roux et al. 2017, unpublished data). A full guild of predators is present in HiP, including lions *Panthera leo*, leopards *Panthera pardus*, spotted hyenas *Crocuta crocuta*, and cheetahs *Acinonyx jubatus*.

Hwange National Park is located in Western Zimbabwe (19°00'S, 26°30'E). The study area is located in the eastern section of the park and covers c. 2000 km². The vegetation is dominantly bushy, characteristic of semiarid dystrophic savannas, but interspersed with large patches of open grasslands (Chamaillé-Jammes et al. 2006). Grasslands, where about 30 artificial waterholes are located (Chamaillé-Jammes et al. 2009a, Courbin et al. 2016), and open areas (i.e. grasslands and bushed grasslands) represent 5.11 % and 21.76 % of the landscape in the park respectively (Arraut et al. 2018). The annual rainfall averages 600 mm with most rains falling between November and April during the rainy season (Chamaillé-Jammes et al. 2006). In the dry season, pumped waterholes become the only source of water available and form attractive and profitable areas for water-dependent animals such as plains zebra. Predation pressure is high as lions are abundant (i.e. around 3.5 individuals 100 km⁻²) (Loveridge et al. 2016) and other predators such as leopards, spotted hyenas, wild dogs and cheetahs are present in lower densities. In the study area, plains zebra density has been fluctuating around 1 individual km⁻² from 2004 until now (Chamaillé-Jammes et al. 2009b, Grange et al. 2015, unpublished data).

Plains zebra populations are made of two basic social units: harems and bachelor groups (Klingel 1969b, Estes and Otte 2012). Non-territorial, the harems are composed of a stallion and most often several adult females (unrelated, as females disperse from their natal groups when they are around 2 years-old (y.o.)), subadults of both sexes, and dependent offspring. Harem sizes range between 2 and 13 individuals (median: 5 individuals) in HiP, and between 2 and 10 individuals (median: 5 individuals) in HNP, and are positively correlated to the number of reproductive females in harems, both in HiP (Spearman rank correlation: $r_s = 0.86$, $N = 135$, $P < 0.001$) and HNP (Spearman rank correlation: $r_s = 0.89$, $N = 51$, $P < 0.001$). Males that are not stallions form all-male bachelor groups, which range between 1 and 9 individuals (median: 3.5 individuals) in HiP, and between 1 and 19 individuals (median: 3 individuals) in HNP, and sometimes attempt to take over a stallion's position. In harems, young males and females

disperse when they are around 2 y.o.: dispersing females join already existing harems or form a new group with a bachelor, and males join bachelor groups. Reproductive females may also change group but this is rare: in this study, 92% (N = 453) and 95% of mares (N = 290) were still in the same harem after one year, and 86% (N = 342) and 97% (N = 76) after two years, in HNP and HiP respectively. Harems and/or bachelor groups frequently aggregate in larger unstable groups (referred to as 'herds' hereafter), defining a multi-layered social system (Klingel 1969b).

Data collection

The demographic monitoring of the populations started in 2004 in HNP and 2017 in HiP. Observations were made twice a year, once in the wet season (between November and April) and once in the dry season (between May and October). These monitoring periods are hereafter referred to as 'sessions'. During these sessions, we determined group composition and identified new individuals. In HiP, all zebra groups in the park are monitored, while in HNP only a subset of groups is monitored in the eastern section of the park. The zebras were identified by their unique stripe patterns and were categorized into four age-classes: foal, from birth to 1 y.o.; yearling, between 1 and 2 y.o.; subadult, between 2 and 4 y.o.; and adults, 4 y.o. and older. Subadult and adult females are hereafter referred to as 'reproductive females'. The age of previously unobserved young individuals was estimated using Penzhorn's criteria (Penzhorn 1982) combined with photos of foals of known age and we used suckling behaviour as criteria to determine motherhood (as in Barnier et al. 2012). More details about the demographic monitoring protocol can be found in Grange et al. (2015). Although the composition of some harems had been monitored since 2007 in HNP, data on the composition of herds were only available in 2018-2019 for this population. For HiP, we used data on the composition of harems and herds collected in 2017-2020.

Data analysis

In both populations, we investigated whether the number of reproductive females in harems affected the probability for harems to be observed (i) alone (analysis 1), (ii) in herd with at least another harem, but no bachelors (analysis 2), and (iii) in herd with at least one bachelor group (analysis 3). We did so by fitting generalized linear mixed models with logit links and a binomial distribution for errors. As a response variable, the models included the probability for harems to be observed alone (coded '1') vs. in herd (coded '0') for analysis 1, the probability for harems to be observed in herd with at least another harem (coded '1') vs. alone or in herd with at least one bachelor group (coded '0') for analysis 2, and the probability for harems to be observed in herd with at least one bachelor group (coded '1') vs. alone or in herd with at least another harem

(coded '0') for analysis 3. For the three analyses, the models included the number of reproductive females in harems, the season, and the interaction between both, as fixed effects. The identity of the harem was included as a random effect to take into account harem differences in their tendency to associate with other groups. For HiP, but not for HNP, we had access to a 20-m resolution vegetation cover map (Appendix S1). We used it to compute the mean vegetation cover in a buffer of increasing radius (0 to 2500 m, by 50 m increments) around the locations of harems (ranging between 0 for completely open vegetation, and 1 for completely closed vegetation). For HiP, we therefore fitted the above described models with cover as an additional fixed effect predictor, fitting one model per radius. As we fitted models in a Bayesian framework (see below), we compared models with data from different radius using the Widely Applicable Information Criterion (WAIC, recommended by Vehtari, Gelman, & Gabry, 2017) (Appendix S2). The best models were then interpreted and are the ones presented in the main text for HiP. We reported Area Under the Curve (AUC) values for the selected models to provide an estimate of their quality.

We then tested, in both populations, whether the probability of stallion turnover increases with the number of reproductive females in harems (analysis 4). We used the same method as the one used in Vitet et al. (submitted) for the plains zebra population of HNP. Stallion turnover was considered to have occurred if a harem was seen during two consecutive sessions with a different stallion at each session. For this analysis, we did not use information when the resighting of a harem occurred more than a year later (i.e. when the harem was not seen in two consecutive sessions) as there was too much uncertainty about how the number of reproductive females had changed during this period. In total, we observed 13 turnovers out of 197 possible occasions where it could have occurred (i.e. when a harem is seen during a session and re-observed within a year, regardless of the stallion identity) in the HiP population (N = 96 harems), and 30 turnovers out of 232 possible occasions where it could have occurred in the HNP population (N = 31 harems). For each population, we fitted a generalized linear mixed model with a logit link and a binomial distribution for errors to test the relationship between the likelihood of having observed a stallion turnover (response variable, binary coded '1' for turnover and '0' for no turnover) and the number of reproductive females in the harem at the first session. To account for the fact that turnovers are more likely to occur as time passes, we included an additive effect of the log-transformed number of days between the two sessions. We included the identity of the stallion and the identity of the harem as random effects on the intercept to account for the fact that stallions and harem females could differ in their ability to repel (for stallions) or willingness to accept (for females) an external male.

For all these analyses, we fitted and reported full models, i.e. models integrating the explanatory variables presented above. Models were fitted in a Bayesian framework using Stan (Carpenter et al. 2017) accessed using the *brms* package (Bürkner 2017) in R (R Core Team 2019). We used the non-informative default priors, and for each model ran four chains with 4000 iterations each and checked for convergence and quality of fit using the recommended criteria (visual inspection of trace plot, $R_{hat} < 1$, effective sample size $> 0.5 * \text{post-warmup samples}$, posterior predictive checks) (Conn et al. 2018). We based our assessment of the strength of the relationship between explanatory variables and response variables on the model coefficients and their 95% credible intervals (CrI). As the 95% CrI of some coefficients were largely asymmetric, 0 being at the margin of the intervals, we also reported and based our assessment on the 89% CrI of the model coefficients, as sometimes recommended (Kruschke 2014).

RESULTS

Effect of vegetation cover on the probabilities for harems to be observed alone or in herd

In HiP, vegetation cover has a contrasted influence on the probabilities for harems to be alone or in herd with other zebra groups. The probability for harems to be alone possibly increases slightly as cover increases (Appendix S3: Table S1), and this appears to hold irrespectively of the scale at which the mean vegetation cover around harems is estimated (Appendix S2: Fig. S1B). The probability for harems to be with another harem decreases slightly as vegetation cover increases at small scales (Appendix S3: Table S2), and likely has no effect at larger scales (Appendix S2: Fig. S2B). The probability for harems to be with bachelors decreases strongly (compare effect sizes between Figs. S1B, S2B, S3B in Appendix S2) as vegetation cover increases (Appendix S3: Table S3) at large scales (between 1 and 2 km), and does not seem to be affected at smaller scales (Appendix S2: Fig. S3B). Therefore, for subsequent analyses, we retained models that used mean vegetation cover index estimated at 500 m, 50 m and 1550 m scale for models investigating the effect of the number of reproductive females in harems on the probability for harems to be alone, with other harems, and with at least one bachelor group, respectively (Appendix S2).

Although we could not conduct a similar analysis in HNP, nor include HNP in the analysis, comparisons of the average probabilities for harems to be observed alone, in herd with harems, and in herd with at least one bachelor group between HiP and HNP support these results: areas used by zebras in HNP are generally more open than in HiP, and HNP harems are less often alone and more often in herd (with at least another harem or at least one bachelor group), than in HiP (Fig. 2).

Effect of the number of reproductive females on the probabilities for harems to be observed alone or in herd

In HiP, the number of reproductive females in harems does not influence the probability for harems to be found alone or with other harems (Fig. 2A; Appendix S3: Tables S1, S2). However, in the wet season, the probability for harems to be found with bachelors decreases as the number of reproductive females in harems increases, and this possibly also hold true in the dry season (Fig. 2A; Appendix S3: Table S3). Those results hold irrespectively of the scale at which the mean vegetation cover around harems is estimated (Appendix S2: Figs. S1C, S2C, S3C).

In HNP, the number of reproductive females in harems has no or only a marginal effect on how harems associated with other zebra groups (Fig. 2B; Appendix S4). During the dry season, there are non-significant tendencies for harems to be more often alone and less often with bachelors as the number of reproductive females in harems increases (Fig. 2B; Appendix S4: Tables S1, S3). This is not the case in the wet season, and the number of reproductive females has no influence on whether harems were found with other harems in any season (Fig. 2B; Appendix S4: Table S2).

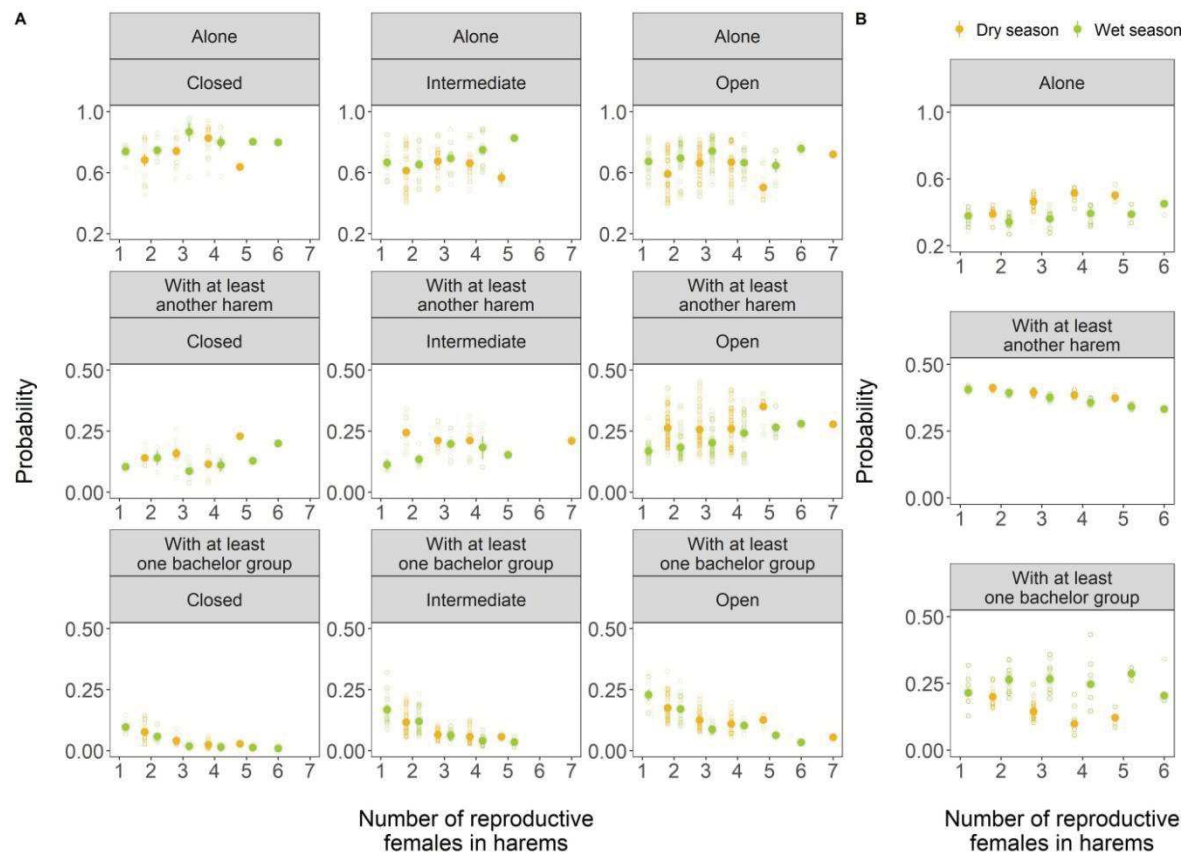


Figure 2. The probability for harems to be observed alone, in herd with at least another harem but no bachelors, or in herd with at least one bachelor group as a function of the number of reproductive females in harems, season and habitat openness (‘Closed’, ‘Intermediate’ and ‘Open’ for mean vegetation cover ≥ 0.2 , between 0.1 and 0.2, and < 0.1 around the locations of harems, respectively) in the HiP population (A), and as a function of the number of reproductive females in harems and season in the HNP population (B). For HiP, the vegetation cover around harems was estimated as the mean vegetation cover in a buffer of 500 m, 50 m, and 1550 m around the locations of harems for models investigating the effect of the number of reproductive females in harems on the probability for harems to be alone, in herd with at least another harem, and in herd with at least one bachelor group, respectively. The open circles show the predictions from the models for all observations of the dataset, and the filled circles represent the mean \pm SE of these values.

Effect of the number of reproductive females on the probability of stallion turnovers in harems

In the HiP population, the average probability of a stallion turnover between two sessions does not increase with increasing number of reproductive females in harems (Appendix S5: Table S1), and is particularly low at ~ 0.02 (Fig. 3A).

On the opposite, in HNP, the average probability of a stallion turnover between two sessions increases with the number of reproductive females in harems (Appendix S5: Table S2), varying from 0.03 to 0.43 for harems which have from 1 to 5 reproductive females (Fig. 3B).

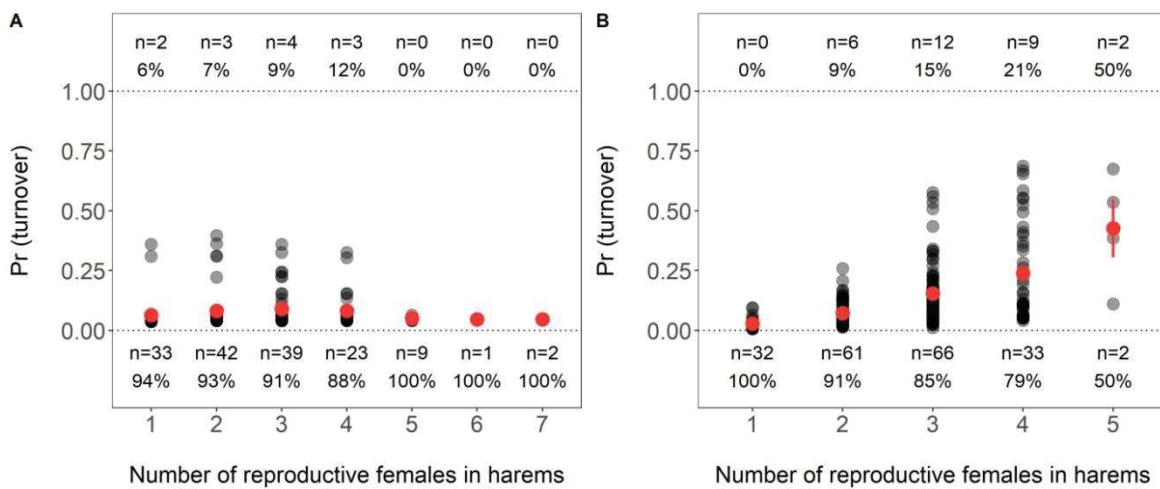


Figure 3. The probability of a stallion turnover between two consecutive sessions as a function of the number of reproductive females in harems at the first session, in HiP population (A) and HNP population (B). The black dots show the predictions from the models for all observations of the dataset, with the mean \pm SE of these values shown in red. For each category of the number of reproductive females, we also report the sample size (also expressed as percentage of observation for the category) of turnover (1) or no turnover (0).

DISCUSSION

Our study shows that the number of reproductive females in plains zebra harems is not an important driver of harem-harem associations, whereas it seems to have some influence on the probability that harems are observed with bachelor groups: harems with more reproductive females seems to be found less often near bachelors groups, although significant uncertainty remains, especially in HNP. Additionally, we show that associations of groups are more common in open vegetation, being especially true for harem-bachelors associations for which largely open areas clearly make associations more likely. Overall, this suggests that harems including many reproductive females may seek to avoid bachelors, and actually seem to have more success in doing it in HiP where vegetation is overall more closed than in HNP. In accordance with this, we found that, in HiP, and contrary to what was observed in HNP, the probability of stallion turnovers in harems does not increase with the number of reproductive females in harems.

No effect of harem size on the probability for harems to be observed alone

The number of reproductive females in harems is a strong proxy of harem sizes, and we had predicted that, if diluting predation risk through aggregation is important, smaller harems would be found more often with other zebra groups. This was not observed in HiP and HNP. One possible explanation for this result is that predation is not a strong driver of associations between groups. However, this hypothesis is unlikely as zebras in both sites experience high predation pressure (Grange et al. 2015, Le Roux et al. 2019) and results from different studies suggest that zebra herd sizes tend to increase as predation risk increases in HNP (Valeix et al. 2009) and other populations (Thaker et al. 2010, Creel et al. 2014) (but see Stears et al. 2020 for contrasting results in HiP and other areas). Another hypothesis which seems more likely to explain the fact that larger harems are not observed more often alone than smaller ones is that larger harems do not benefit from a reduced predation risk. This hypothesis is supported by the fact that harem size was found to have no significant effect on individual vigilance and on the survival of adults and foals in the plains zebra population of HNP (Vitet et al., accepted in *Ecosphere*), which suggests that dilution and detection effects may not always occur.

No effect of harem size on the probability for harems to be observed with other harems

In HNP, the probability of stallion turnover increases with the number of reproductive females in harems (Vitet et al., submitted), suggesting that these harems are preferentially targeted by bachelors that are looking to secure mating opportunities. This may lead these harems to associate: in plains zebra, associated stallions are more efficient at preventing incursions of bachelors in their harems than a single stallion (Rubenstein 1986) and accordingly, Rubenstein and Hack (2004) found that stallions herd together (with their harems) as the bachelor pressure increases in order to reduce the risks that bachelors represent in terms of female harassment and stallion turnover. Such benefit was also documented in non-human primate species where males collectively defend their one-male units against bachelor males (Pappano et al. 2012, Xiang et al. 2014). Therefore, we expected harems with many reproductive females to be more likely to be observed in herd with other harems than harems with fewer reproductive females, but results do not support our prediction. We see several potential explanations for this unexpected result: (1) it could be that harems with few reproductive females, even if they are not exposed to a high threat from bachelors, gain some benefits and/or incur so few costs at associating with other harems that herds should form. This was suggested by Rubenstein and Hack (2004) who found that the foraging rate of males and females is not significantly reduced for harems in herd with other harems, in comparison to lonely harems; (2) alliances between stallions from different harems do

not exist. Indeed, Linnartz and Linnartz-Nieuwdorp (2017) reported that dominant Konik stallions *Equus ferus* from different groups do not work together to repel bachelors, and several studies reported coalitions between stallions in equids but these coalitions implied stallions from a same harem: usually, the dominant stallion leads the mares away from bachelors while the subordinate stallion approaches and challenges the bachelor males (e.g. feral horses *Equus ferus*: Feh 1999, Linklater and Cameron 2000, Linnartz and Linnartz-Nieuwdorp 2017). This could question the existence of intergroup stallion alliances. In such case, larger harems, if they are more attractive for bachelors, may tend to isolate themselves rather than rely on harem-harem coalitions to reduce the higher bachelor threat they are exposed to. Note however that several studies reported coalitions between stallions from different harems in plains zebra (Rubenstein 1986, Rubenstein and Hack 2004, Silver 2014) which makes this hypothesis unlikely in this species; (3) larger harems with many reproductive females are more difficult for the stallion to drive towards other harems. Indeed, the presence of many reproductive females in a harem may lead to a higher level of conflict in terms of group decision-makings given the different nutritional needs links to pregnancy and lactation (Fischhoff et al. 2007a). This hypothesis was proposed by Silver (2014) who found that, when the threat from bachelors increases, plains zebra harems with more adult females establish fewer bonds with other harems than harems with few adult females. If stallions holding large harems have more difficulties at driving the movement of their harems, this could explain why we found that larger harems with many reproductive females are not found more often with other harems than harems with fewer reproductive females.

Larger harems avoid herding with bachelors and efficiently reduce their risk of stallion turnovers

As expected, we found that harems with many reproductive females are less likely to be observed in herd with at least one bachelor group than harems with few reproductive females in HiP. This result supports our prediction that larger harems could avoid to herd with bachelor groups in order to reduce the risk of stallion turnovers and of cuckoldry that bachelors pose. Indeed, several studies found that males that tend one or more females are sometimes unable to prevent extra-group matings and paternities (ungulates: Clutton-Brock et al. 1982, Hogg 1984; see references in Isvaran and Clutton-Brock 2007 for other mammalian taxa), and spatial proximity between breeding females and breeding males have been shown to increase the reproductive success of these latter (e.g. eastern grey kangaroos *Macropus giganteus*: Montana et al. 2020; fallow deer *Dama dama*: Apollonio et al. 1989). Therefore, it could be particularly risky for stallions to have bachelors in the vicinity of their harems. Accordingly, we found that the probability of stallion turnovers does not increase with increasing number of reproductive females in harems in HiP,

thus suggesting that the strategy of harems with many reproductive females to avoid bachelors is efficient at reducing the risk of stallion turnover in these harems.

In HNP, we found that harems with many reproductive females tend to be less often observed in herd with at least one bachelor group than harems with fewer reproductive females but this tendency was only observed in the dry season and is non-significant. In the wet season, harems with more reproductive females do not tend to be less often observed with bachelors, implying that larger harems may fail at avoiding bachelors during that period of the year. This could be due to the fact that there may be more receptive females in harems during the wet season. Indeed, although zebras breed year round (Wackernagel 1965, Barnier et al. 2012), births occur mostly in the wet season (Smuts 1976b) and female can be receptive soon after foaling (Wackernagel 1965, King 1965, Barnier et al. 2012). Thus, larger harems may be even more attractive for bachelors and this, combined with the fact that harems in HNP may have fewer possibilities to avoid bachelors due to the habitat which is globally more open than in HiP, may explained why the probability for harems to be observed in herd with bachelors tend to decrease as the number of reproductive females in harems increases in HNP only during the dry season. One way to validate this hypothesis would be to investigate whether stallion turnovers occur mostly in the wet season. However, data available do not allow to known accurately when stallion turnovers occurred: we only know that stallion turnovers between two sessions are more frequent from wet to dry seasons (57%, N = 17) than from dry to wet seasons (43%, N = 13). Therefore, this explanation remains hypothetical.

Habitat openness facilitates the formation of herds

Within HiP, we found that the probability for harems to be observed alone possibly increases slightly as vegetation cover increases, and that their probability to be observed in herd with at least one bachelor group strongly decreases as vegetation cover increases. Between populations, results show that the probability for harems to be observed alone is globally higher and their probability to be observed in herd is globally lower in HiP (Fig. 2A) than in HNP (Fig. 2B). Overall, these results support our prediction that open areas facilitate herd formations, as found in other studies (Gerard et al. 1993, 2002, Gerard and Loisel 1995, Pays et al. 2007a, Isvaran 2007, Fortin et al. 2009). In HiP, the habitat is generally more closed, with open areas scarcer than in HNP, at least in the northern section, and the park is virtually free of artificial waterholes. Overall, this could reduce the probability for groups to associate with one another in this park and make harems less visible for bachelors. At the contrary, open areas are common in HNP, which could increase the distance at which groups may perceive each other, and there are few artificial

waterholes around which zebra groups tend to aggregate. Another hypothesis to explain the difference found between HiP and HNP is that social pressures may differ between the two study sites. If the density of bachelor groups to harems is high, harems may have more difficulties at avoiding bachelors. However, the ratio of bachelor groups to harems is similar between the two populations: 0.165 in HiP (N = 170 and N = 1029 observations of bachelor groups and harems, respectively), and 0.178 in HNP (N = 127 and N = 712 observations of bachelor groups and harems, respectively). Therefore, this hypothesis is improbable, and the difference in habitat openness between HiP and HNP is more likely to explain the variations observed between the two populations in terms of probabilities for harems to be alone or in herd with other zebra groups.

CONCLUSION

This study suggests that the number of reproductive females in harems and vegetation cover both influence associations between plains zebra groups, especially the associations between harems and bachelor groups, with consequences for stallion turnovers. This work adds to a corpus of studies which identified factors shaping encounter rates between conspecific individuals/groups (e.g. Fortin et al. 2009, Vander Wal 2011, Vander Wal et al. 2014, Peignier et al. 2019) and overall expands our vision of the drivers of spatial associations between groups within populations.

ACKNOWLEDGMENTS

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APPENDIX S1

We created a vegetation cover map of HiP using a supervised classification of Pleiade satellite images obtained thanks to the GEOSUD program (<http://ids.equipex-geosud.fr/>). Acquisition dates of the 3 images were 2016-08-10 (one image, covering the northern Hluhluwe section) and 2016-02-19 (two images, covering the center and the southern iMfolozi section). The classification was done using the QGIS Semi-Automatic Classification (SAC) plugin (Congedo 2013), version 6.2.9.

Using the SAC plugin first required us to define a set of training areas, i.e. patches that are homogenous with regards to the vegetation characteristics to be mapped. Each training area is attributed a category or value for the characteristics. The approach we used here was to find training areas of very low woody cover, given a cover value of 0, and training areas of very high woody cover, given a value of 1. All were defined by the same person (GF) for consistency. We then used the maximum likelihood algorithm to classify all pixels. We therefore obtained a binary classification of all pixels, each pixel representing a 2*2 m area, the spatial resolution of Pleiades images. We then converted the 2-m resolution map into a 20-m resolution map, averaging the cover values within each 20*20 m pixel. This average measure could therefore be interpreted as a cover density. We noted that sometimes dense areas would have a few pixels of open areas spread out, leading us to defined a threshold (here, 0.8) above which the 20*20 m was assumed to be of very high woody cover (1). Overall, this general approach allowed us to classify the study area along a gradient of vegetation cover at the 20-m resolution, which we deemed suitable for studies focused on zebra spatial behaviour.

The park is made of two regions that differ greatly in topography and vegetation, which made it difficult to obtain a satisfying classification global classification in one step. We therefore made two distinct classifications: one for the hilly Northern section, based on 37 training areas, and one for the flatter South, based on 20 training areas. We then stitched the predictions for these two regions to obtain one global map.

APPENDIX S2

In the HiP population, an additive effect of the mean vegetation cover around the locations of harems was included in the generalized linear mixed models which investigated whether the number of reproductive females in harems affected the probability for harems to be observed (i) alone (analysis 1), (ii) in herd with at least another harem, but no bachelors (analysis 2), and (iii) in herd with at least one bachelor group (analysis 3). To determine the scale at which vegetation cover was most likely to influence the response variable, we used a vegetation cover map (Appendix S1) to compute the mean vegetation cover in a buffer of increasing radius (0 to 2500 m, by 50 m increments) around the locations of the harems. We then refitted the models with cover as an additional fixed effect predictor, fitting one model per radius. For each analysis, we compared the models ($N = 51$) with data from different radius using Widely Applicable Information Criterion (WAIC) : smaller WAIC values indicate better predictive models (Vehtari et al. 2017).

For analysis 1, the selected model was the one including an additive effect of vegetation cover calculated as the mean vegetation cover in a buffer of 500 m around the location of harems (Fig. S1A), although we acknowledge that the differences between the WAIC values of the models were small (range: 922.738 – 925.454, Fig. S1A). Note however that considering other buffer distances do not qualitatively change the conclusions: the effect of vegetation is only slightly less pronounced when considering larger scales (Fig. S1B), the effect of the number of reproductive females in harems is not affected by the buffer distance considered (Fig. S1C), and the same observation is made for the interactive effect of the number of reproductive females in harems and season (Fig. S1D).

For analysis 2, the selected model was the one including an additive effect of vegetation cover calculated as the mean vegetation cover in a buffer of 50 m around the location of harems (Fig. S2A), although we admit that the differences between the WAIC values of the models were small (range: 804.429 – 808.357, Fig. S2A). Note however that the effect of the number of reproductive females in harems is not affected by the buffer distance used (Fig. S2C), as is the interactive effect of the number of reproductive females in harems and season (Fig. S2D). This is not the case for the effect of vegetation cover which becomes positive when considering larger scales (Fig. S2B), so we recognize that using another buffer distance may lead to a different result than the one presented in this study and that this latter may be interpreted carefully.

For analysis 3, the selected model was the one including an additive effect of vegetation cover calculated as the mean vegetation cover index in a buffer of 1550 m around the location of

harems (Fig. S3A), although we acknowledge that the differences between the WAIC values of the models were small (range: 475.815 – 482.308, Fig. S3A). However, considering other buffer distances do not qualitatively change the conclusions. Indeed, although the effect of vegetation cover is more or less pronounced depending on the scale considered, the coefficient for this effect is almost always negative (except when considering shorter scales, Fig. S3B). Moreover, the effect of the number of reproductive females in harems is not affected by the buffer distance considered (Fig. S3C), as is the interactive effect of the number of reproductive females in harems and season (Fig. S3D).

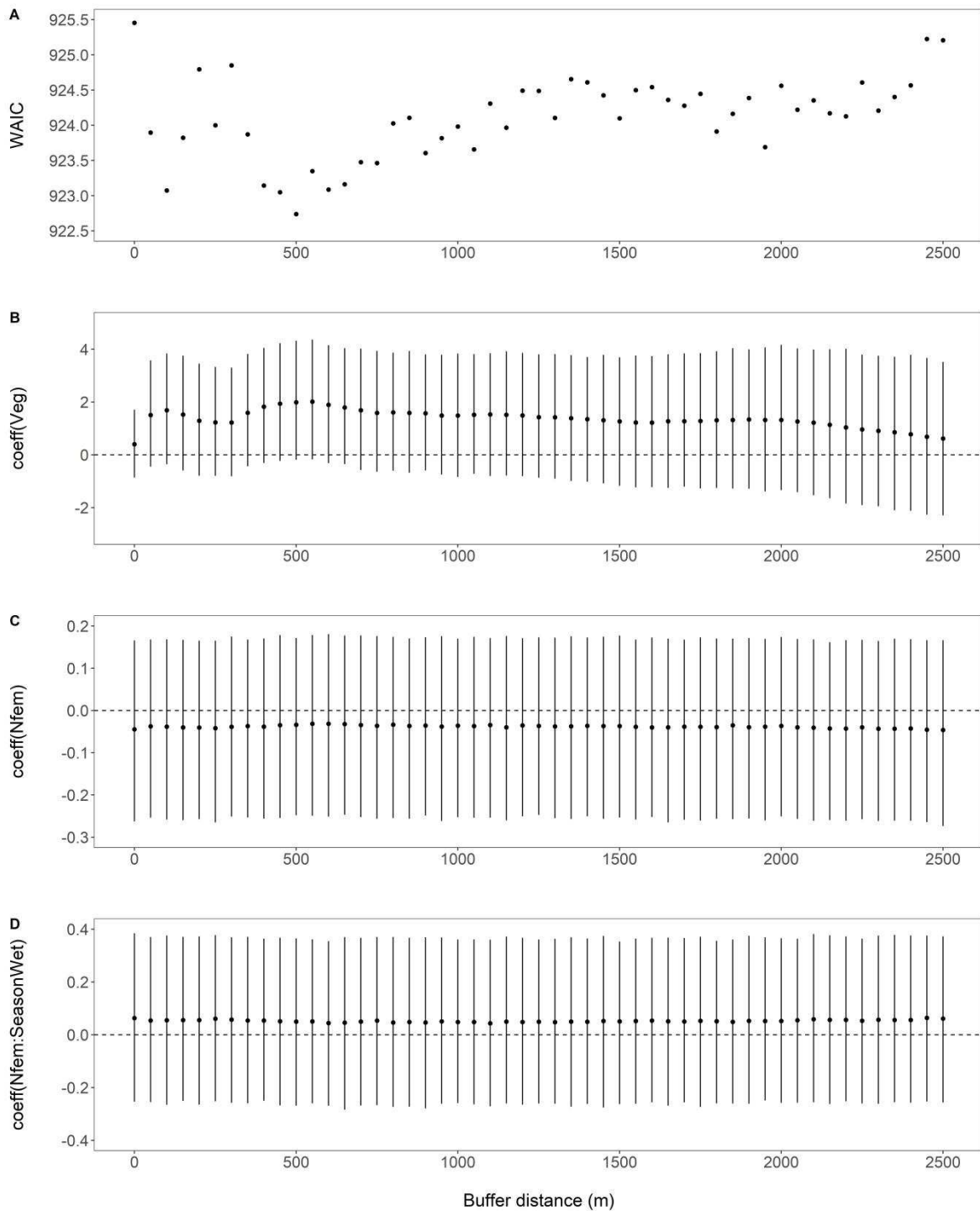


Figure S1. Values of Widely Applicable Information Criterion (WAIC) (A), and coefficients and 95% credible intervals for the effect of vegetation (coeff(Veg)) (B), for the effect of the number of reproductive females in harems (coeff(Nfem)) (C), and for the interactive effect of the number of reproductive females in harems and season ($\text{coeff(Nfem:SeasonWet)}$) (D) for the 51 models fitted for the probability for harems to be observed alone in relation to the buffer distance (m) used to determine the mean vegetation cover around harems.

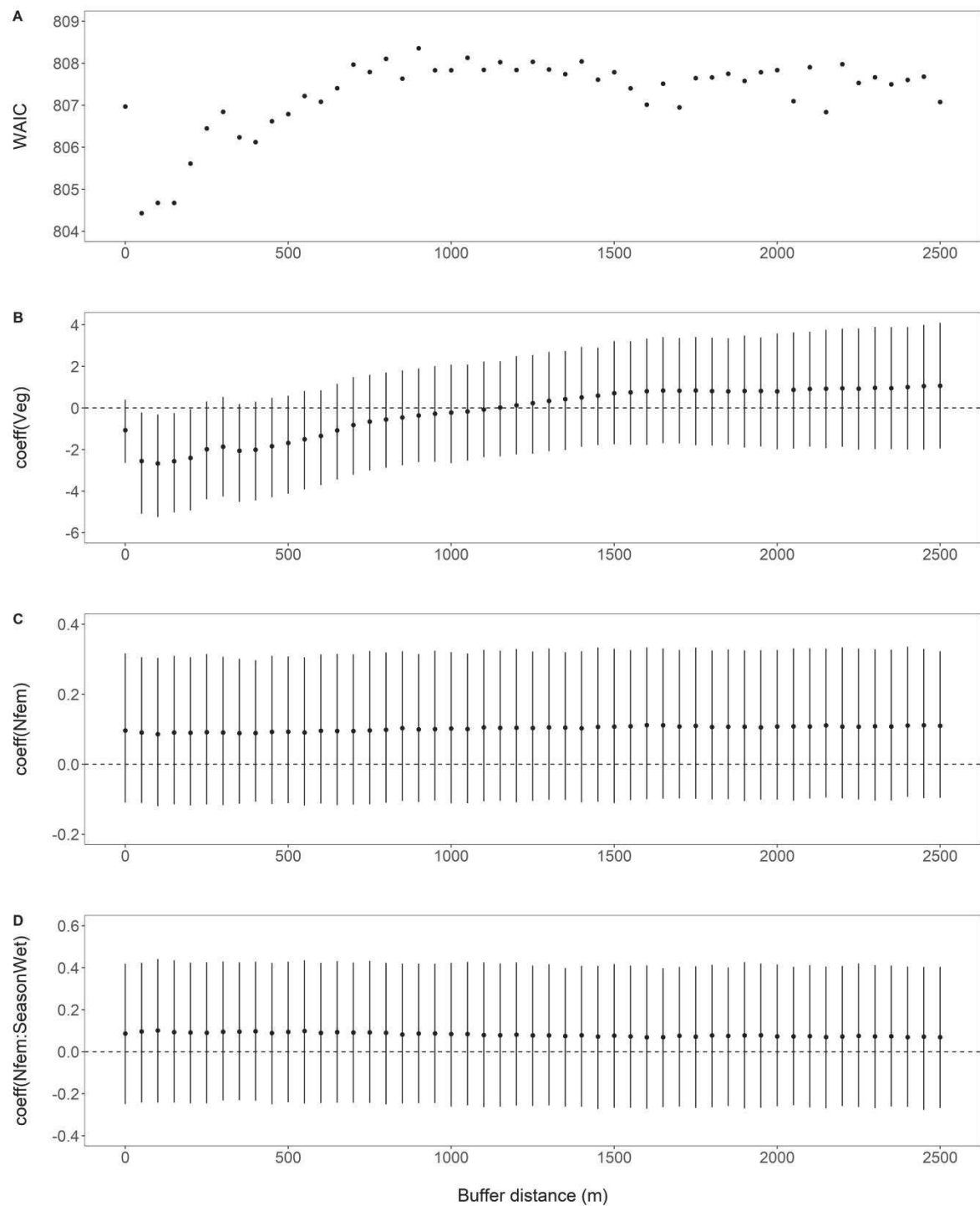


Figure S2. Values of Widely Applicable Information Criterion (WAIC) (A), and coefficients and 95% credible intervals for the effect of vegetation (coeff(Veg)) (B), for the effect of the number of reproductive females in harems (coeff(Nfem)) (C), and for the interactive effect of the number of reproductive females in harems and season ($\text{coeff(Nfem:SeasonWet)}$) (D) for the 51 models fitted for the probability for harems to be observed in herd with at least another harem in relation to the buffer distance (m) used to determine the mean vegetation cover around harems.

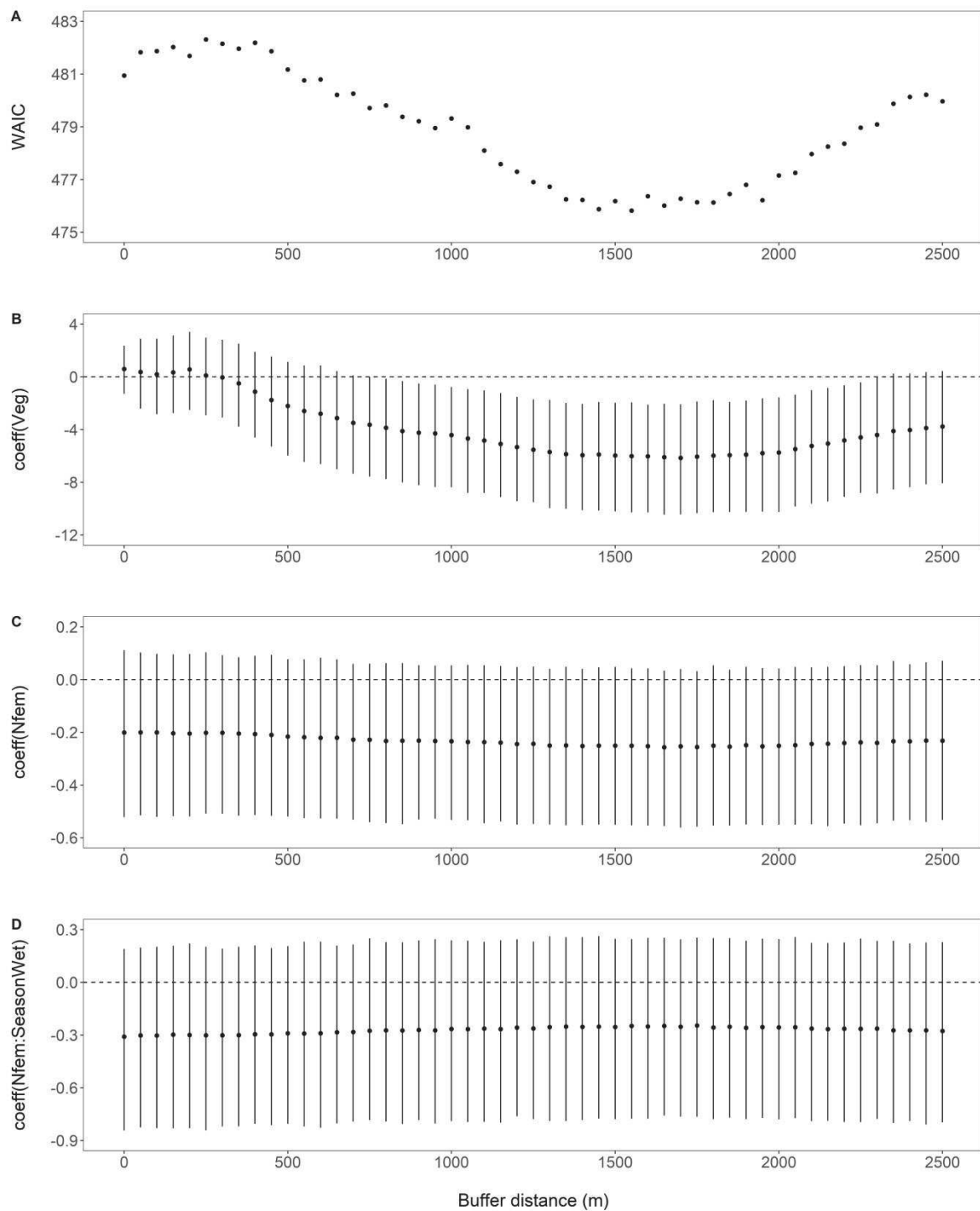


Figure S3. Values of Widely Applicable Information Criterion (WAIC) (A), and coefficients and 95% credible intervals for the effect of vegetation (coeff(Veg)) (B), for the effect of the number of reproductive females in harems (coeff(Nfem)) (C), and for the interactive effect of the number of reproductive females in harems and season ($\text{coeff(Nfem:SeasonWet)}$) (D) for the 51 models fitted for the probability for harems to be observed in herd with at least one bachelor group in relation to the buffer distance (m) used to determine the mean vegetation cover around harems.

APPENDIX S3

In HiP, we fitted generalized linear mixed models to investigate the effect of the number of reproductive females in harem, season, and vegetation cover (i.e. mean vegetation cover around the locations of harems) on the probability for harems to be observed alone (Table S1), in herd with at least another harem (Table S2), and in herd with at least one bachelor group (Table S3).

Table S1. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed alone in the HiP population. Variables are: the number of reproductive females (N_{fem}), season (Season, dry, wet), and vegetation cover (i.e. mean vegetation cover in a buffer of 500 m around the harem) (Veg) as fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.85	0.55 – 1.17	0.59 – 1.09
Population-level ('fixed') effects	Intercept	0.55	-0.13 – 1.24	0.01 – 1.11
	N_{fem}	-0.04	-0.25 – 0.18	-0.21 – 0.14
	Season_wet	0.14	-0.76 – 1.06	-0.60 – 0.89
	Veg	2.01	-0.12 – 4.28	0.26 – 3.84
	$N_{\text{fem}} : \text{Season_wet}$	0.05	-0.26 – 0.36	-0.19 – 0.33

* $AUC = 0.794$

Table S2. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed in herd with at least another harem in the HiP population. Variables are: the number of reproductive females (N_{fem}), season (Season, dry, wet), and vegetation cover (i.e. mean vegetation cover in a buffer of 50 m around the locations of harems) (Veg) as fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.66	0.27 – 1.04	0.36 – 0.97
Population-level ('fixed') effects	Intercept	-1.31	-2.03 – -0.66	-1.86 – -0.77
	N_{fem}	0.09	-0.12 – 0.32	-0.08 – 0.27
	Season_wet	-0.59	-1.63 – 0.41	-1.37 – 0.28
	Veg	-2.57	-5.07 – -0.29	-4.55 – -0.64
	$N_{\text{fem}} : \text{Season_wet}$	0.10	-0.24 – 0.44	-0.18 – 0.37

* $AUC = 0.764$

Table S3. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed in herd with at least one bachelor group in the HiP population. Variables are: the number of reproductive females (N_{fem}), season (Season, dry, wet), and vegetation cover (i.e. mean vegetation cover in a buffer of 1550 m around the locations of harems) (Veg) as fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.72	0.13 – 1.29	0.27 – 1.21
Population-level ('fixed') effects	Intercept	-0.96	-2.04 – 0.03	-1.81 – -0.12
	N_{fem}	-0.25	-0.56 – 0.04	-0.49 – -0.01
	Season_wet	0.49	-0.80 – 1.81	-0.52 – 1.60
	Veg	-6.01	-10.17 – -1.93	-9.38 – -2.67
	N_{fem} : Season_wet	-0.25	-0.78 – 0.25	-0.67 – 0.16

* $AUC = 0.818$

APPENDIX S4

In HNP, we fitted generalized linear mixed models to investigate the effects of the number of reproductive females in harems and season on the probability for harems to be observed alone (Table S1), in herd with at least another harem (Table S2), and in herd with at least one bachelor group (Table S3).

Table S1. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed alone in the HNP population. Variables are: the number of reproductive females (N_{fem}) and season (Season, dry, wet) as interactive fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.36	0.05 – 0.69	0.09 – 0.61
Population-level ('fixed') effects	Intercept	-0.72	-1.48 – 0.01	-1.32 – -0.10
	N_{fem}	0.17	-0.08 – 0.41	-0.04 – 0.36
	Season_wet	0.05	-0.84 – 1.00	-0.70 – 0.80
	$N_{\text{fem}} : \text{Season_wet}$	-0.12	-0.43 – 0.18	-0.36 – 0.13

Table S2. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed in herd with at least another harem in the HNP population. Variables are: the number of reproductive females (N_{fem}) and season (Season, dry, wet) as interactive fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.13	0.01 – 0.39	0.00 – 0.27
Population-level ('fixed') effects	Intercept	-0.26	-0.94 – 0.41	-0.83 – 0.27
	N_{fem}	-0.05	-0.28 – 0.17	-0.24 – 0.13
	Season_wet	-0.03	-0.88 – 0.83	-0.70 – 0.67
	N_{fem} : Season_wet	-0.02	-0.31 – 0.26	-0.25 – 0.21

Table S3. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability for harems to be observed in herd with at least one bachelor group in the HNP population. Variables are: the number of reproductive females (N_{fem}) and season (Season, dry, wet) as interactive fixed effects, and the identity of the harem (ID(Harem)) as a random effect. The estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Harem)	0.57	0.20 – 0.96	0.27 – 0.87
Population-level ('fixed') effects	Intercept	-0.99	-2.07 – 0.05	-1.82 – -0.12
	N_{fem}	-0.29	-0.65 – 0.08	-0.58 – 0.01
	Season_wet	-0.39	-1.64 – 0.86	-1.44 – 0.59
	N_{fem} : Season_wet	0.38	-0.05 – 0.82	0.01 – 0.72

APPENDIX S5

We fitted generalized linear mixed models to investigate the effect of the number of reproductive females in harem and the log-transformed number of days between the two sessions on the probability of stallion turnover between two sessions in HiP (Table S1) and HNP (Table S2).

Table S1. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability of stallion turnover between two sessions ($\Pr_{(\text{turnover})}$) in the HiP population. Variables are: the number of reproductive females (N_{fem}) and the log-transformed number of days between the two sessions ($\log(\text{Days})$) as fixed effects, and identities of the stallion ($\text{ID}(\text{Stallion})$) and of the harem ($\text{ID}(\text{Harem})$) as random effects. Estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Stallion)	2.12	0.09 – 6.21	0.00 – 4.07
	ID(Harem)	1.75	0.10 – 4.58	0.01 – 3.26
Population-level ('fixed') effects	Intercept	-7.04	-21.17 – 2.22	-15.70 – 1.89
	N_{fem}	0.12	-0.80 – 1.27	-0.65 – 0.91
	$\log(\text{Days})$	0.39	-1.26 – 2.42	-1.15 – 1.73

Table S2. Coefficients of the mixed model investigating the effect of the number of reproductive females in a harem on the probability of stallion turnover between two sessions ($\Pr_{(\text{turnover})}$) in the HNP population. Variables are: the number of reproductive females (N_{fem}) and the log-transformed number of days between the two sessions ($\log(\text{Days})$) as fixed effects, and identities of the stallion ($\text{ID}(\text{Stallion})$) and of the harem ($\text{ID}(\text{Harem})$) as random effects. Estimates, 95% credible intervals (95% CrI), and 89% credible intervals (89% CrI) are shown.

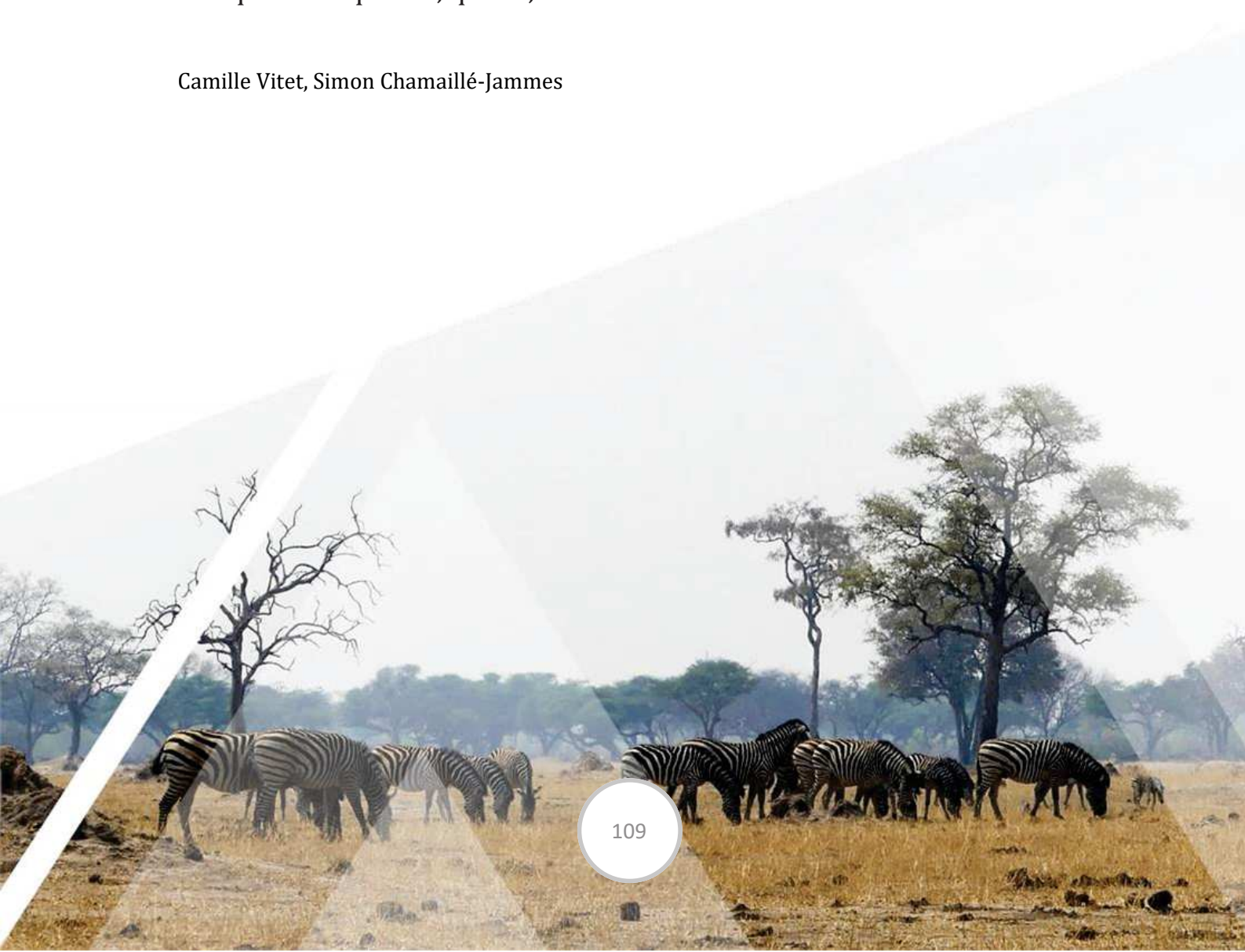
Effect type	Coefficient	Estimate	95% CrI	89% CrI
Group-level ('random') effects	ID(Stallion)	1.60	0.39 – 3.19	0.54 – 2.71
	ID(Harem)	0.55	0.02 – 1.57	0.00 – 1.10
Population-level ('fixed') effects	Intercept	-15.15	-25.00 – -7.21	-22.43 – -8.41
	N_{fem}	1.25	0.60 – 2.05	0.65 – 1.83
	$\log(\text{Days})$	1.79	0.43 – 3.38	0.62 – 2.96

ANALYSE COMPLÉMENTAIRE ET PRÉLIMINAIRE

Herd formations between pairs of harems in the multilevel society of plains zebra: how long do they last, and how often, when and where do they occur?

Formations de troupeaux entre paires de harems au sein d'une société multi-niveaux de zèbre des plaines : combien de temps durent-elles, et à quelle fréquence, quand, et où ont-elles lieu ?

Camille Vitet, Simon Chamailé-Jammes



ABSTRACT

In multilevel societies, stable social units frequently aggregate with one another in higher hierarchical tiers, forming larger unstable herds (i.e. when at least two groups aggregate). The dynamic of herd formations is thought to be modulated by the costs and benefits of grouping and environmental conditions (e.g. protection against predators, competition, resource availability, habitat structure) which vary in time and space. Plains zebras *Equus quagga* live in multilevel societies composed of only two tiers, with two basic social units - harems (i.e. single-male family groups) and bachelor groups (i.e. all-male groups) - that frequently aggregate into larger unstable herds. However, to our knowledge, little is known about the dynamic of herd formations between pairs of harems in this species. In this study, we used GPS data from the plains zebra population of Hwange National Park (HNP, Zimbabwe) to document the duration, the frequency, and the spatial and temporal distribution of fusion events (i.e. herd formation events) between dyads (i.e. pairs of harems) in this species. Overall, the main results of this preliminary analysis show that (i) dyads don't stay long together, (ii) shared space-use is not a strong determinant of the likelihood for dyads to merge and of the proportion of time they spent together, (iii) fusion events are more frequent and dyads spent a higher proportion of their time together in the wet season than in the dry season, (iv) in times of water scarcity, locations where dyads are together occur closer to pumped waterholes than locations where they are not together, and (iv) pairs of harems seem to associate in herd mostly during the night, to merge mostly at dawn and dusk, and to stay for longer periods of time together during the night than during the day, overall suggesting that pairs of harems herd mostly in times of high predation risk. Globally, this study helps improve our knowledge of the dynamic of herd formations between pairs of harems in the multilevel society of plains zebras.

KEYWORDS: association patterns, dyadic interactions, home range overlap, multilevel society, predation, seasonality

INTRODUCTION

Among the many different social systems that exist in the animal kingdom, multilevel societies are thought to be one of the most complex ones (Clutton-Brock 2016, Ward and Webster 2016, Grueter et al. 2017b). In such societies, stable core social units move through the environment and frequently aggregate with one another in a higher hierarchical tier, forming herds (i.e. when at least two groups aggregate) that vary in size and composition over time and can reach several hundred individuals (Grueter et al. 2017b). Multilevel societies differ from other forms of fission-fusion social systems in the sense that herds, when separating, split into their social subunits that are generally socially cohesive and sometimes clearly spatially delimited (Grueter et al. 2012), while in fission-fusion systems, herds split in subgroups of variable size, composition, and cohesiveness (Aureli et al. 2008).

Multilevel societies have been described in several species such as African elephant *Loxodonta africana* (Wittemyer et al. 2005, Couzin 2006), prairie dogs *Cynomys ludovicianus* (Hoogland 1995), vulturine guineafowl *Acryllium vulturinum* (Papageorgiou et al. 2019), sperm whales *Physeter microcephalus* (Whitehead et al. 2012), Asian colobines *Rhinopithecus* spp. (Kirkpatrick and Grueter 2010, Grueter et al. 2017a), hamadryas baboons *Papio hamadryas* (Schreier and Swedell 2009), and geladas *Theropithecus gelada* (Snyder-Mackler et al. 2012). Associating temporarily with other groups can provide some benefits such as a better protection against predators (Rubenstein 1986, Schreier and Swedell 2009, Tong et al. 2015, Lin et al. 2020), thermoregulatory advantages (Nowzari et al. 2013) and a reduction of the amount of female harassment by bachelor males and takeover and infanticide risks (the bachelor threat hypothesis; Rubenstein 1986, Rubenstein and Hack 2004, Pappano et al. 2012). Decisions of groups to associate in herd has also been shown to be driven by resource distribution (Cortés-Avizanda et al. 2011, Rimbach et al. 2014, Pinacho-Guendulain and Ramos-Fernández 2017) and habitat structure (Gerard and Loisel 1995, Gerard et al. 2002, Pays et al. 2007a, Isvaran 2007, Fortin et al. 2009) for example. The amount of shared space-use may also be a determinant of whether groups will associate or not (Chaverri et al. 2007, Best et al. 2014; but see De Villiers and Kok 1997, Carter et al. 2009), although other factors such as kinship and individuals social preferences have been shown to play a role as well (Frère et al. 2010, Carter et al. 2013).

Plains zebras live in multilevel societies composed of only two tiers, with two basic social units - harems and bachelor groups - that frequently aggregate into larger unstable herds (Klingel 1967, 1969b, Rubenstein and Hack 2004, Estes and Otte 2012). Non-territorial harems are composed of a stallion (i.e. harem-male) and most often several adult females, subadults of both

sexes, and dependent offspring; and males that are not harem-males form all-males bachelor groups. Herds of plains zebra can vary greatly in size (from two to 100 groups) and composition (containing harems only, or harems and bachelor groups) (Rubenstein and Hack 2004). Rubenstein and Hack (2004) investigated how the sizes of plains zebra herds in the Laikipia region (Kenya) were affected by (i) the presence of cuckolding males in the vicinity of herds, (ii) predation risk, and (iii) availability of food resources: they found that the main determinant of herd size was the pressure of intruding, and potentially cuckolding, bachelor males in the vicinity of herds (as this latter increases, the sizes of herds increase). However, to our knowledge, little is known about the dynamic of zebra herd formations between pairs of harems (i.e. hereafter referred to as 'dyads') in other areas; and the duration, frequency, spatial and temporal distribution of these herd formation events (i.e. hereafter referred to as 'fusion events') are poorly documented in this species.

In this study, we used GPS data from the plains zebra population of Hwange National Park (HNP, Zimbabwe) to determine fusion and fission events among dyads. We determined the duration of fusion events and tested the effect of seasonal home range overlap (HRO) on the frequency of these events and on the proportion of time dyads spent together. Moreover, we investigated the distance travelled by dyads during fusion events and the displacement between the locations where dyads merge (i.e. fusion) and split (i.e. fission) in relation to the duration of the fusion events. Finally, we assessed the spatial and temporal distribution of the fusion events.

We tested the prediction that the number of fusion events per month per dyad and the proportion of time dyads spent together increase as the HRO between the pair of harems which constitutes the dyad increases. We also expect the distance travelled by dyads when they are together and the displacement between the locations where dyads merge and split to be small if dyads aggregate around resources, and to be large if dyads are in transit. Indeed, zebras have been shown to reduce their travel rate once they encounter a grazing patch (Brooks 2005). To assess the spatial distribution of fusion events, we tested the prediction that, in the late dry season (i.e. between August and October), locations where dyads are together are recorded closer to pumped waterholes than locations where dyads are not together, as water is only available at pumped waterholes during that period of the year and this scarcity may increase the probability that dyads merge near water sources. Finally, to assess the temporal distribution of fusion events, we tested the prediction that fusion events are more frequent in the dry season, as food and water resources become scarce, which could constrain plains zebra groups to associate in the few patches of resources available. We then focused on the temporal distribution of fusion events across the diel cycle and investigated how fusion locations distribute between hours of the

day, which are more or less risky in terms of predation. We did not test for a difference between seasons as predation risk by lions has been shown to vary mostly between hours of the day rather than between seasons: lions are mostly nocturnal (Schaller 1972) and herbivores are therefore exposed to a higher risk of predation during the night and also at dawn and dusk (Valeix et al. 2009). We therefore tested the prediction that, during the night and at dawn and dusk (i.e. risky times), locations where dyads merge and are together are more frequent, and dyads stay for a longer period of time together than during the day, assuming that increasing group size bring anti-predator benefits.

MATERIAL AND METHODS

Study site and species

The study was conducted in the eastern section of HNP in Western Zimbabwe over an area covering c. 2000 km² (19°00'S, 26°30'E). The vegetation is dominantly bushy, characteristic of semiarid dystrophic savannas, but interspersed with patches of open grasslands (Chamaille-Jammes et al. 2006). The annual rainfall averages 600 mm, with most rains falling between November and April (Chamaille-Jammes et al. 2006). In the hot dry season (i.e. between August and October), water is only available in a limited number of artificial waterholes where groundwater is pumped into. In the study area, these pumped waterholes allow water-dependent species, such as plains zebra, to have access to water year-around. Predation pressure is high as lions *Panthera leo* are abundant (i.e. around 3.5 individuals 100 km⁻²) (Loveridge et al. 2016) and leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, and spotted hyenas *Crocuta crocuta* are also present.

We used plains zebra as a model species. In the study area, plains zebra density has been fluctuating around 1 individual km⁻² from 2004 until now (Chamaillé-Jammes et al. 2009b, Grange et al. 2015, unpublished data). Plains zebra populations are made of two basic social units: harem and bachelor groups (Klingel 1969b, Estes and Otte 2012). Non-territorial harems are composed of a stallion (i.e. harem-male) and most often several adult females, subadults of both sexes, and dependent offspring. Males that are not harem-males form all-males bachelor groups. In harems, young males and females disperse when they are around 2 years-old: females join already existing harems and males join bachelor groups. Subadult and adult females can also change group, but this is rare: 92% of mares (N = 453) were still in the same harem after one year, and 86% (N = 342) after two years. Harems and bachelor groups frequently aggregate into larger unstable herds that

can vary greatly in size (from two to 100 groups) and composition (containing harems only, or harems and bachelor groups) (Rubenstein and Hack 2004).

Data collection and analysis

Between 2009 and 2017, 34 adult females, each from a different harem, were equipped with Global Positioning System (GPS) collars. For the analysis, we only kept individuals with a minimum of 2000 GPS locations recorded and with intervals of 1 hour (h) or 30 minutes (m) between GPS location acquisitions. We only kept dyads with temporal and spatial overlap, a necessary condition for fusion events to occur. To determine if dyads overlap spatially, we estimated seasonal home ranges (HR) based on the 95% kernel utilization density distribution during the dry and wet seasons for each year. HRO were estimated by computing Bhattacharyya's affinity index from *adehabitathR* package (Calenge 2006) in R software (R Core Team 2019). The index can take values from 0 (no overlap) to 1 (identical space use). HRO among dyads ranges between less than 1% and 89.48% (mean = 25.27%, median = 19.63%). To determine fission and fusion events, we calculated the distance between synchronous locations (i.e. GPS locations recorded at the same time for the pairs of harems that composed the dyads) for every dyad which HR overlapped (HRO > 0). In total, we had N = 615608 synchronous locations for which distances between dyads (N = 117) vary from less than 1 m to 82.6 km in the wet season (mean = 21.46, median = 18.13), and from less than 1 m to 71.8 km in the dry season (mean = 17.26, median = 13.65) (Fig. 1).

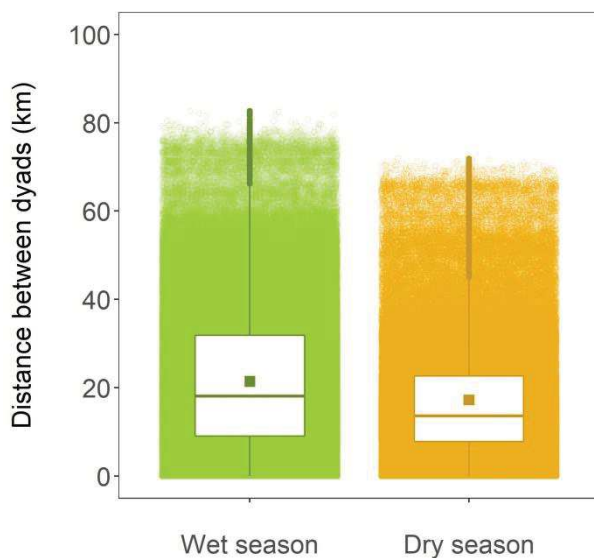


Figure 1. Distance between dyads (in km) in wet (green) and dry (orange) seasons for dyads which overlap spatially (HRO > 0) and temporally (i.e. synchronous locations). The open circles give the observed values (N = 615608) and are jittered for clarity. Boxplots show the median of the distances and the lower and upper hinges (corresponding to the first and third quartiles). Squares represent the mean distance between dyads for each season.

Two harems (i.e. represented by two collared females) were considered to be in a herd if they were less than 100 m apart, a distance threshold used in others ungulate species (Childress and Lung 2003). If the dyad merged, then split during less than two hours (i.e. corresponding to one and three GPS locations for collars with 1 h and 30 m data acquisition intervals respectively), and merged again, we considered that the two harems have remained together all along. This allows correcting for the fact that GPS errors could occurred and that dyads could sometimes slightly move more than 100 m away from each other for insignificant periods of time. Following the method used by Wielgus et al. (2020), we created for each dyad a binary vector with value '1' when dyads were together (i.e. when the two harems are 100 m away from each other or less), and '0' when they are not (i.e. when the two harems are more than 100 m away from each other). This allows us to calculate the proportion of time dyads spent together, the spatial and temporal distribution of the fusion events and how long dyads stay together (i.e. number of consecutive time steps where dyads are together). We only kept fusion events with at least two consecutive time steps where dyads are together, as fusion events including only one location where dyads are together (N = 1208) may not necessarily reflect the formation of a herd, and including them in the analysis would have led to an under-estimation of how long dyads stay together. Therefore, in total, we had N = 2242 fusion events that lasted more than an hour (N = 79 dyads).

We estimated the number of fusion events per dyad per month by dividing the total number of fusion events by the number of months during which the two harems that composed the dyads were simultaneously tracked. The proportion of time dyads spent together was calculated as the number of locations where the two harems were together, divided by the total number of synchronous locations recorded for the dyad. We also investigated the effect of the duration of the fusion events on the distance travelled by dyads during the fusion event and their displacement from the location where they merged. Distance travelled during fusion events was calculated as the sum of the distance between each location of the fusion event. Displacement was calculated as the distance between the location where dyads merge and the location where dyads split. Finally, we used the GPS locations of the pumped waterholes present in the study area (N = 48) to calculate the distance to the closest waterhole for locations where dyads are not together and locations where dyads are together, in the late dry season.

We fitted generalized linear models (i) with a Poisson distribution of errors to assess the effect on home range overlap and season on the number of fusion events per dyad per month, and (ii) with a binomial distribution of errors to determine if home range overlap and season affect the proportion of time dyads spent together. To investigate the effect of the time dyads spent together and season on the distance they travelled together and their displacement, we

fitted generalized linear models with a Poisson distribution of errors. For this analysis, two observations were considered to be outliers and were therefore removed from the analysis : the time dyads spent together ranges between 2 h and 69 h, except for two observations where dyads spent 116 h and 136 h together. We considered that data supported an effect of an explanatory variable when the Akaike Information Criterion corrected for small sample sizes (AICc) of a model including it was smaller by at least 2 units than the one of a simpler model without the variable (therefore considering only informative parameters, *sensu* Arnold 2010).

RESULTS

On average, dyads stayed together during 6.22 h (median = 4, max = 136) and they stayed together for slightly longer periods of time in the dry season (mean = 7.00, median = 5, max = 54) than in the wet season (mean = 6.07, median = 4, max = 136) (Fig. 2).

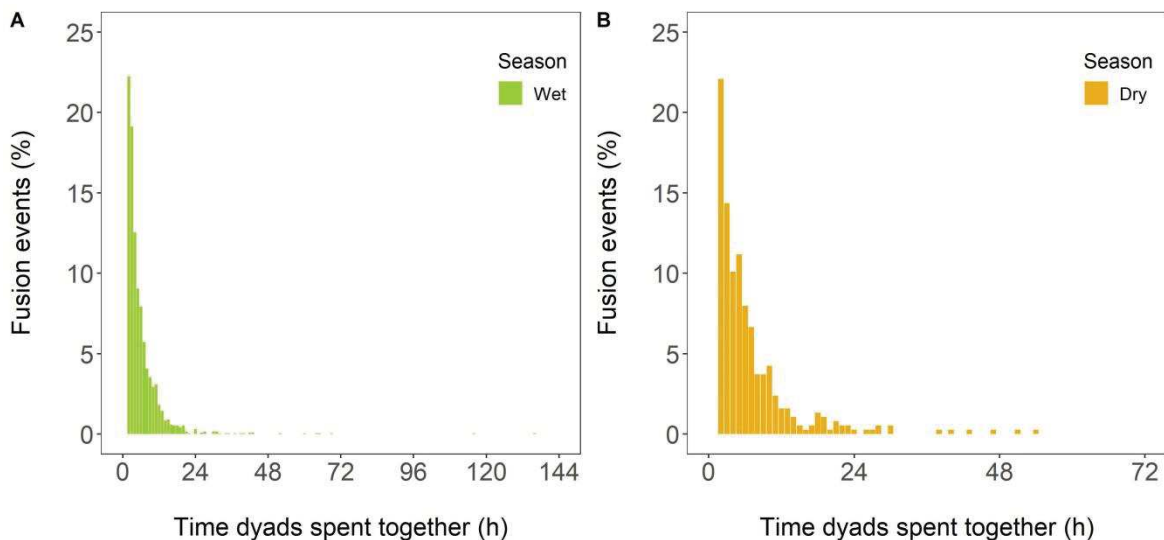


Figure 2. Proportion of fusion events for each class of time dyads spent together (in h) in the wet season (A) and the dry season (B).

We found that the number of fusion events per month per dyad is related to their HRO (Table 1). As expected, fusion events tend to be more frequent as the HRO of the dyads increases (Fig. 3A), although there is a high variability: it ranges from 0 to 36 fusion events per month when HRO is high (around 0.75) (Fig. 3A). Similarly, we found that dyads spend a higher proportion of their time together when their HRO increases (Table 2, Fig. 3B), although there is a high variability: the proportion of time dyads spent together ranges between 3.59% and 52.94% when HRO is high (around 0.75). Therefore, home-range overlap is a poor predictor of the likelihood for dyads to merge and of the proportion of time they spend together.

The number of fusion events per month per dyad and the proportion of time dyads spend together are related to seasons (Tables 1-2): fusion events are more frequent and dyads spend a higher proportion of their time together in the wet season than during the dry season (Fig. 3).

Table 1. Statistics of models investigating the effect of HRO and season on the number of fusion events per month per dyad (N_{fusion}). Models could include the effects of the overlap between the seasonal home ranges of dyads (*HRO*) and season (*Season*, dry or wet) as fixed effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. The number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), delta-AICc (Δ -AICc), deviance, and marginal R-squared values (R^2m) are shown.

Model	n	AICc	Δ -AICc	Deviance	R^2m
$N_{\text{fusion}} \sim HRO * Season$	4	2036.31	0.00	2028.31	0.80
$N_{\text{fusion}} \sim HRO + Season$	3	2059.03	22.68	2053.03	0.72
$N_{\text{fusion}} \sim HRO$	2	2250.97	214.58	2246.97	0.66
$N_{\text{fusion}} \sim Season$	2	2932.60	896.21	2928.60	0.41
$N_{\text{fusion}} \sim 1$	1	3136.71	1100.30	3134.71	

Table 2. Statistics of models investigating the effect of HRO and season on the proportion of time dyads spent together ($Pr_{\text{(time together)}}$). Models could include the effects of the overlap between the seasonal home range of dyads (*HRO*) and season (*Season*, dry or wet) as fixed effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. The number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), delta-AICc (Δ -AICc), deviance, and marginal R-squared values (R^2m) are shown.

Model	n	AICc	Δ -AICc	Deviance	R^2m
$Pr_{\text{(time together)}} \sim HRO * Season$	4	22172.33	0.00	22164.32	0.35
$Pr_{\text{(time together)}} \sim HRO + Season$	3	22185.06	12.69	22179.06	0.34
$Pr_{\text{(time together)}} \sim HRO$	2	25237.00	3064.60	25233.00	0.28
$Pr_{\text{(time together)}} \sim Season$	2	47052.19	24879.79	47048.20	0.05
$Pr_{\text{(time together)}} \sim 1$	1	48944.62	26772.19	48942.62	

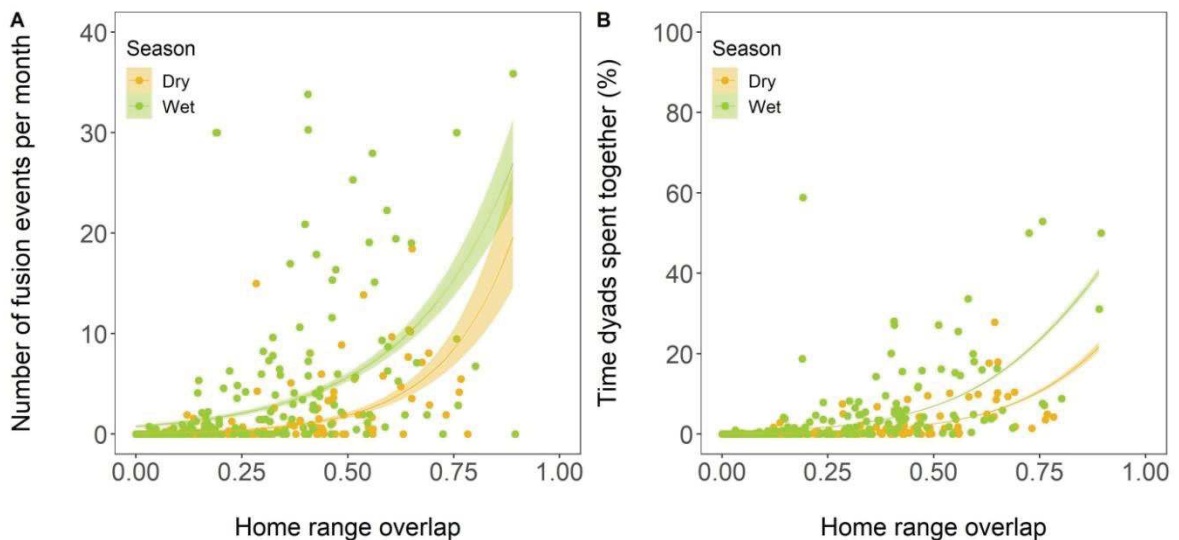


Figure 3. Number of fusion events per month per dyad (A) and proportion of time dyads spent together (B) in relation to HRO in wet (green) and dry (orange) seasons. Dots represent the observed values for each dyad per year and season. Model predictions (solid lines) and 95% confidence envelopes are shown.

We found that, in both seasons, the longer the harems of a dyad stay together, the greater distance they travel together (Fig. 4A, Table 3). For observations where dyads stayed together for 24h or less ($N = 2202$), the average distance travelled by dyads is slightly higher in the dry season (mean = 1.26, median = 0.68) than in the wet season (mean = 0.73, median = 0.44), but overall remains very small as dyads rarely travel more than a few km together (Fig. 4A). Results also show that displacement increases as the duration of fusion events increases (Fig. 4B, Table 4), although there is a high variability: for example, it ranges between 0.02 and 11.10 km for dyads that stayed together more than 24h (Fig. 4B). For observations where dyads stayed together for 24h or less ($N = 2202$), displacement is on average slightly higher in the dry season (mean = 0.82, median = 0.49) than in the wet season (mean = 0.40, median = 0.26). Globally, dyads rarely move together further than a few km of where they merged (Fig. 4B). Note that, overall, the effects of the time dyads spent together and season explained only a small amount of the variability in the distances travelled by dyads and their displacements (R^2 in Tables 3-4).

Table 3. Statistics of models investigating the effect of the time dyads spent together and season on the distance travelled by dyads when they are together (Distance). Models could include the effects of the time dyads spent together (*TimeTogether*) and season (*Season*, dry or wet) as fixed effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. The number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), delta-AICc (Δ -AICc), deviance, and marginal R-squared values (R^2m) are shown.

Model	n	AICc	Δ -AICc	Deviance	R^2m
Distance ~ <i>TimeTogether</i> + <i>Season</i>	3	3787.67	0.00	3781.65	0.16
Distance ~ <i>TimeTogether</i> * <i>Season</i>	4	3789.40	1.73	3781.38	0.16
Distance ~ <i>TimeTogether</i>	2	3951.14	163.47	3947.13	0.12
Distance ~ <i>Season</i>	2	5659.35	1871.69	5655.35	0.06
Distance ~ 1	1	5876.12	2088.46	5874.12	

Table 4. Statistics of models investigating the effect of the time dyads spent together and season on the displacement (Displacement). Models could include the effects of the time dyads spent together (*TimeTogether*) and season (*Season*, dry or wet) as fixed effects. A null model with no explanatory variable was also fitted. Bold lettering indicates the selected model. The number of parameters (n), Akaike Information Criterion corrected for small sample sizes (AICc), delta-AICc (Δ -AICc), deviance, and marginal R-squared values (R^2m) are shown.

Model	n	AICc	Δ -AICc	Deviance	R^2m
Displacement ~ <i>TimeTogether</i> + <i>Season</i>	3	2032.07	0.00	2026.06	0.08
Displacement ~ <i>TimeTogether</i> * <i>Season</i>	4	2032.13	0.05	2024.11	0.08
Displacement ~ <i>TimeTogether</i>	2	2213.33	181.25	2209.32	0.03
Displacement ~ <i>Season</i>	2	2249.73	217.66	2245.73	0.06
Displacement ~ 1	1	2457.28	425.20	2455.27	

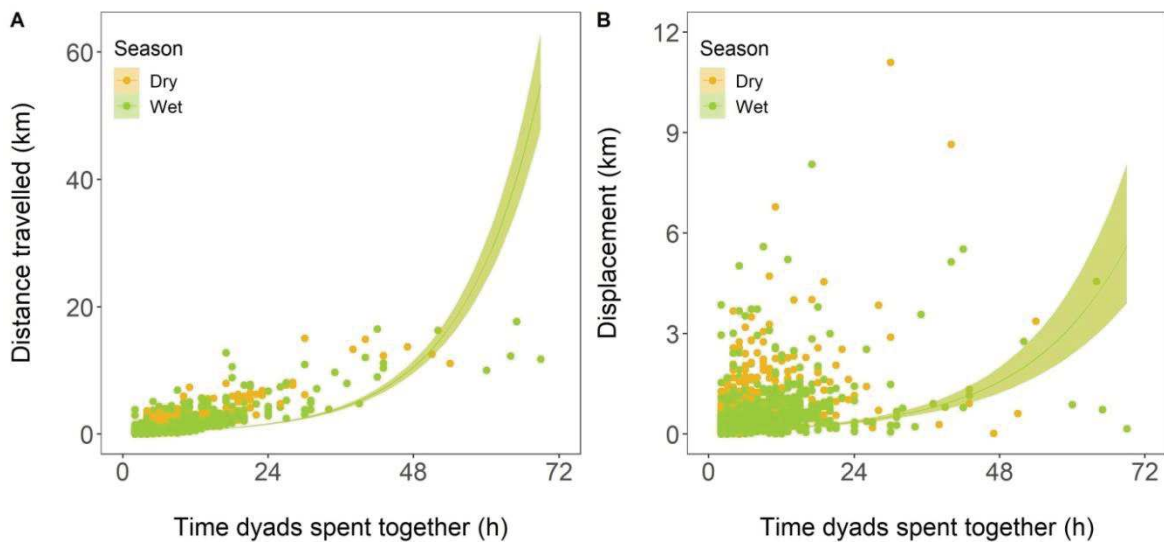


Figure 4. Distance travelled (in km) (A) and displacement (in km) (B) in relation to the time dyads spent together (in h) in wet (green) and dry (orange) seasons. Dots represent the observed values for each dyad per year and season. Model predictions (solid lines) and 95% confidence envelopes are shown.

In the late dry season, when water is only available at pumped waterholes, we found that locations where dyads are together are generally close to water (mean = 1.74, median = 1.33, min = 0.001, max = 7.97), and closer to pumped waterholes than locations where dyads are not together (mean = 4.87, median = 4.19, min = 0.015, max = 27.45) (Fig. 5).

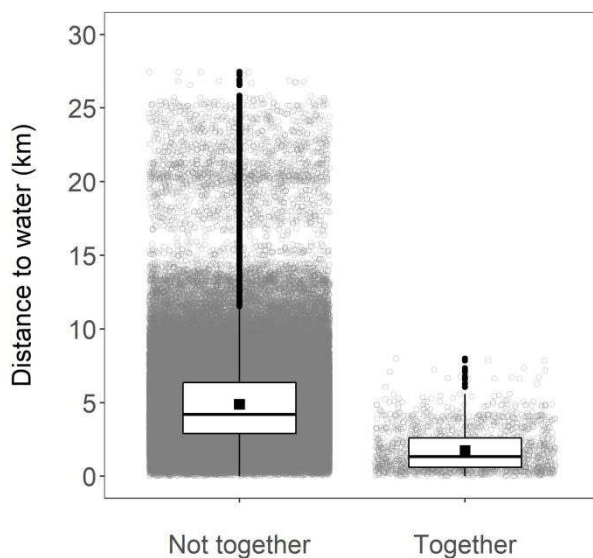


Figure 5. Distance to the closest pumped waterhole (in km) for locations where dyads are not together and where dyads are together. The open circles give the observed values and are jittered for clarity. Boxplots show the median of the distances to water and the lower and upper hinges (corresponding to the first and third quartiles). Squares represent the mean distance to water for locations where dyads are not together and where dyads are together.

Concerning the temporal distribution of fusion events across the diel cycle, we found that locations where dyads are together are recorded in a slightly higher proportion at night than during the day: 53.61% of the fusion locations are recorded between 6 p.m. and 6 a.m. while 46.39% are recorded between 6 a.m. and 6 p.m. (Fig. 6).

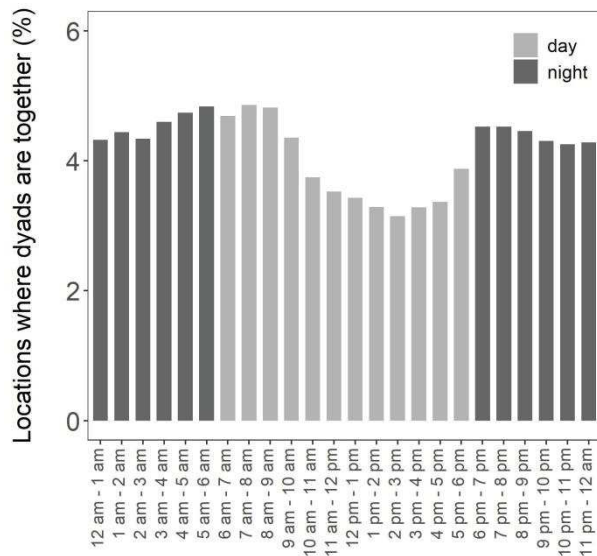


Figure 6. Proportions of the locations where dyads are together recorded across hours of the day, during day (pale grey) and night (dark grey) times.

We also looked at the distribution of the times when dyads merge (i.e. first locations of fusion events) and split (i.e. first locations of fission events) across the diel cycle. Locations where dyads merge occur in a slightly higher proportion at dawn and dusk: 11.37% of the locations where dyads merge are recorded between 6 a.m. and 8 a.m. (i.e. dawn) and 14.99% between 6 p.m. and 8 p.m. (i.e. dusk) (Fig. 7A). The pattern is less clear for the distribution of the times when dyads split (Fig. 7B).

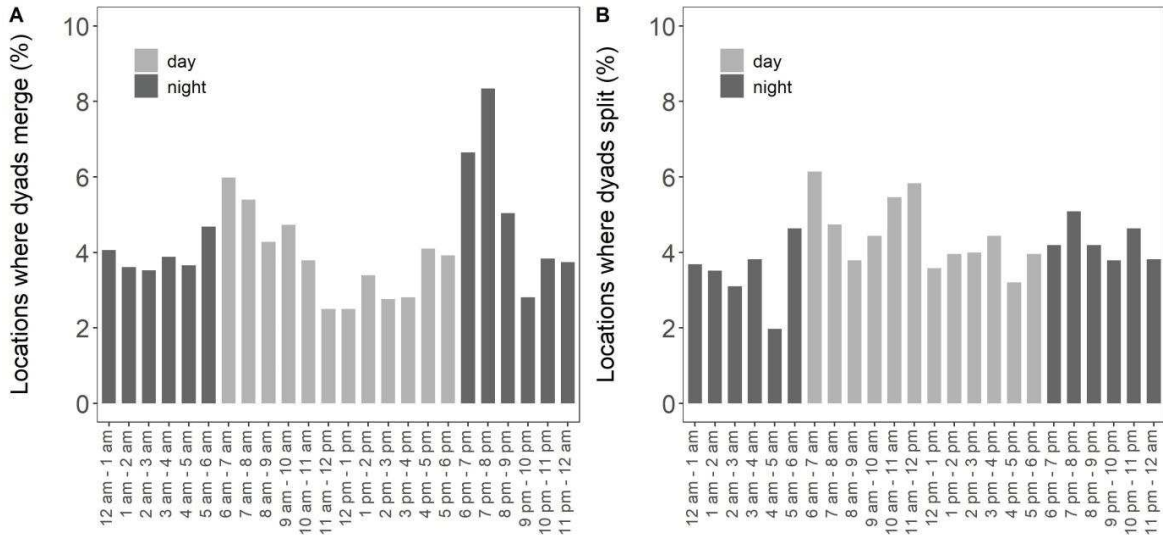


Figure 7. Proportion of locations where dyads merge (i.e. first locations of fusion events) and split (i.e. first locations of fission events) across hours of the day, during day (pale grey) and night (dark grey) times.

We found that the time dyads spent together in relation to the time when they merged is highly variable (Fig. 8A). However, when zooming on a 24h-scale, dyads that merged during the night seem to stay together for slightly longer periods of time than dyads that merged during the day (Fig. 8B). Dyads that merged during the day stay on average 5.89 h together (median = 4), while dyads that merged during the night stay together during 6.51 h on average (median = 5).

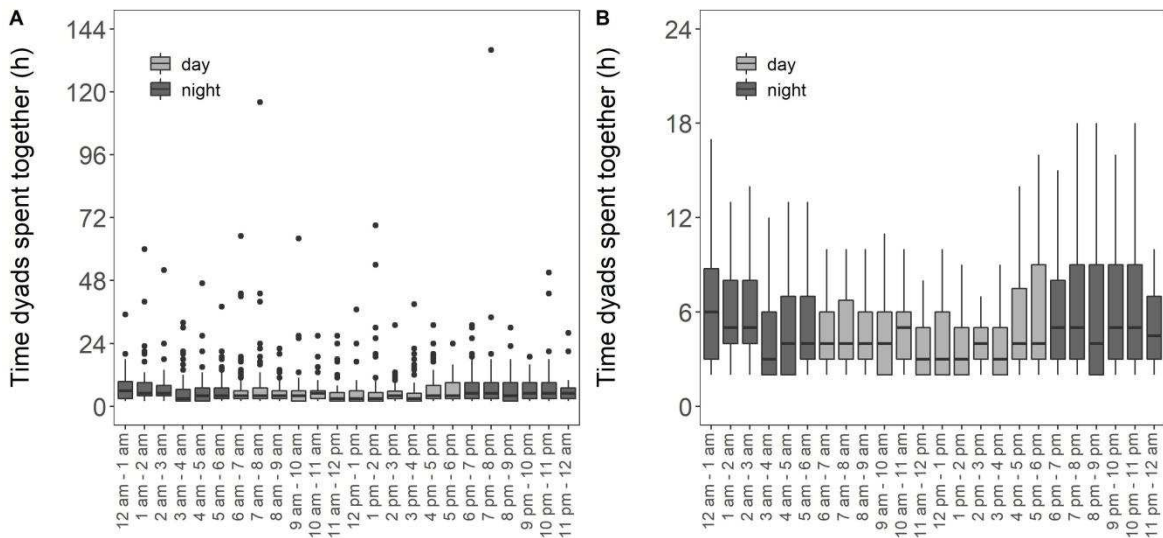


Figure 8. Time dyads spent together (in h) in relation to the time when they merged (A), and the same plot without outliers and the y-axis limited to 24h for better clarity. Boxplots show the median of the time dyads spent together and the lower and upper hinges (corresponding to the first and third quartiles).

DISCUSSION

This study is, to the best of our knowledge, the first to document the duration, frequency and spatial and temporal distribution of herd formations between pairs of harems in the multilevel society of plains zebras. We found that dyads don't stay together for long periods of time, suggesting that there might be some costs at associating with other groups that lead harems to split shortly after they merge. Harems that merged regularly had, as expected, non-negligible HRO, but this overlap remained a poor predictor of the frequency of associations and of the proportion of time dyads spent together. Dyads generally travel together over short distances and not far from where they merged, indicating that associations between dyads could mostly represent aggregations around water and food resources rather than transits. Accordingly, in times of water scarcity, locations where dyads are together occur closer to pumped waterholes than locations where dyads are not together, although harems could merge in the vicinity of waterholes in response to a higher predation risk in these areas as well. Finally, pairs of harems seem to merge when the risk of predation is high (i.e. at night, dawn and dusk) as (i) locations where dyads are together are recorded in a slightly higher proportion at night, (ii) locations where dyads merge are recorded in a higher proportion at dawn and dusk, and (iii) dyads seem to stay for slightly longer periods of time together if they merged during the night than during the day, overall supporting our prediction that harems could associate in response to an increased predation risk.

Our results show that dyads don't stay long together, as pairs of harems stayed together between 6 and 7 hours on average. Although some dyads stayed together for much longer periods, these observations are very anecdotal: only 1.78% of the observations represent dyads which stayed together more than a day. This suggests that there might be some costs to stay in herd for zebras that encourage them to split after few hours. A possible explanation is that groups may differ in their energetic needs, therefore leading to a conflict in decision-makings about where to go (Sueur et al. 2011).

Moreover, although we found that the number of fusion events per dyad per month and the proportion of time dyads spent together is positively related to their HRO, results were highly variable, suggesting that HRO is a poor predictor of the likelihood for dyads to merge and of the proportion of time they spent together. This highlights that other factors than HRO, such as predation risk, resource distribution, and group size, may drive the formation of herds between pairs of harems. Kinship is another potential factor that could encourage pair of harems to associate as Tong et al. (2015) demonstrated that, within herds, kinship between females is higher

than chance in plains zebras of the Laikipia region (Kenya). However, we found that fusion events are more frequent and that dyads, for a given home range overlap, spend a higher proportion of their time together in the wet season than in the dry season, therefore contradicting our prediction that fusion events might be more frequent in the dry season as resources scarcity may constrain groups to associate in the few patches of resources available. It could be that, in the dry season, the low availability of resources increases competition and potentially makes groups more reluctant to associate, as suggested in other species (Masai giraffe *Giraffa camelopardalis tippelskirchii* : Bond et al. 2019; white-fronted geese *Anser albifrons* : Amano et al. 2006). In the wet season, the abundance of resources may allow groups to herd without increasing the competition for access to resources : several studies documented larger group sizes in periods of high food abundance (Isvaran 2007, Phiapalath et al. 2011, Wielgus et al. 2020). A next step would be to combine the GPS data with a vegetation map to test the prediction that locations where dyads are together are recorded mostly in areas where food resources are abundant for zebras (i.e. open grasslands). This would allow testing the relationship between the dynamic of herd formations between pairs of harems and food distribution in this species. Another hypothesis to explain the fact that dyads associate more frequently and spend a higher proportion of their time together in the wet season is that, although zebras breed year round (Wackernagel 1965), there is a birth peak during the wet season (Smuts 1976b). This could encourage harems to merge in order to reduce predation risk for foals, which are known to be preferentially attacked by lions (Stander 1992, Mills and Shenk 1992).

Our results also show that the distance travelled by dyads when they are together and their displacement (i.e. distance between the locations where they merge and split) are both slightly higher in the dry season. This could be due to the fact that, in the wet season, zebras don't need to move over long distances to find a foraging patch as food is highly abundant during this period of the year. Overall, the average distance travelled by dyads do not exceed 2 km in both seasons and dyads rarely move further than a few km of where they merged, suggesting that fusion events could mostly reflect aggregations around water or food resources rather than transits (in that case, dyads would tend to travel over longer distances). Note however that if foraging patches are small, we might have considered the fact that two harems are less than 100 m of each other to be a fusion event while it was not. Accordingly, in time of water scarcity, locations where dyads are together occur on average closer to a pumped waterhole than locations where they are not together (although harems might merge in the vicinity of waterholes in response to an increased predation risk, as these areas are particularly risky (Valeix et al. 2009, 2010)).

Concerning the temporal distribution of fusion events across the diel cycle, we found that (i) locations where dyads are together occur in a slightly higher proportion at night than during the day, (ii) locations where dyads merge occur in a higher proportion at dawn and dusk, and (iii) dyads seem to stay slightly longer together if they merged during the night than if they merged during the day. Overall, this suggests that harems seem to associate in herd when the risk of predation is high, therefore supporting our prediction and results from previous studies which showed that herd sizes tend to increase as predation risk increases in plains zebra (Valeix et al. 2009, Thaker et al. 2010, Creel et al. 2014, but see Stears et al. 2020) and other ungulates species (Molvar and Bowyer 1994, Lingle 2001, Gower et al. 2008, but see Creel and Winnie 2005, Gude et al. 2006). Accordingly, in the late dry season, we found that locations where dyads are together occur closer to a pumped waterhole (which are areas where lions mostly hunt) than locations where they are not together. However, it is difficult to tease apart whether harems merge close to pumped waterholes in that season because the predation risk is high in those areas or because the water scarcity at that period of the year lead to an increased likelihood for harems to join around pumped waterholes. A next step would be to test the prediction, in both dry and wet seasons, that the locations where dyads are together are recorded mostly in areas where predation risk is high (i.e. in the vicinity of waterholes) by combining the GPS data used here with a map representing the distribution of the risk of predation by lions in the area (Courbin et al. 2016).

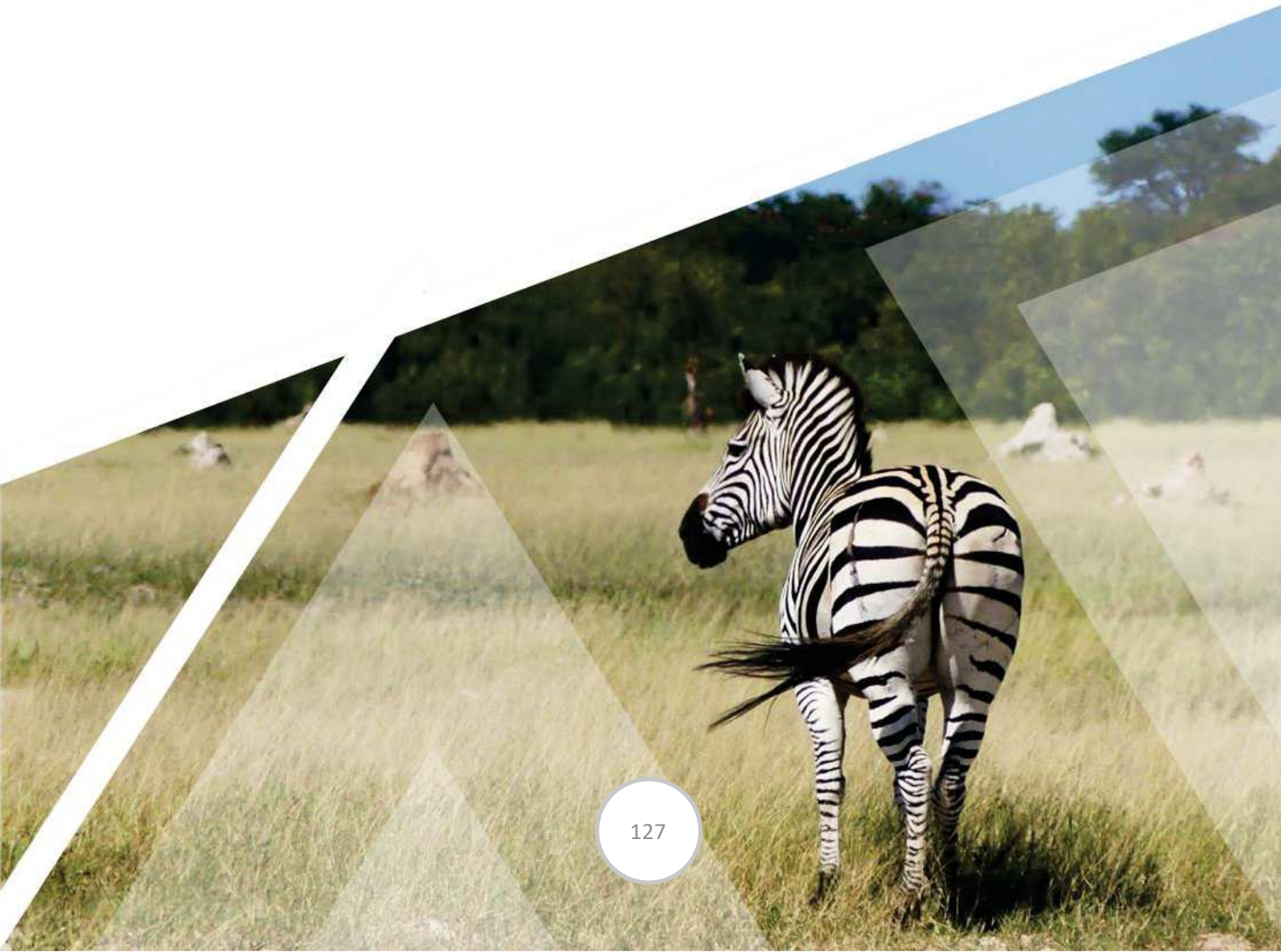
CONCLUSION

To our knowledge, this is the first study to provide a description of the dynamic of association patterns between pairs of harems in plains zebra. The main results of this preliminary analysis show that (i) dyads don't stay long together, (ii) shared space-use is not a strong determinant of the likelihood for dyads to merge and of the proportion of time they spent together, (iii) fusion events are more frequent and dyads spent a higher proportion of their time together in the wet season than in the dry season, (iv) locations where dyads are together occur closer to pumped waterholes than locations where are not together in times of water scarcity, and (iv) dyads seem to associate mostly in times of high predation risk. Overall, this study helps improve our knowledge of the dynamic of associations between pairs of harems and its drivers in the multilevel society of plains zebras.

ACKNOWLEDGMENTS

We thank Elodie Wielgus for sharing some script to run analyses.

DISCUSSION



SYNTHESE

Rappel du contexte

Chez les espèces sociales, la taille des groupes peut avoir d'importants effets sur la dynamique des populations via des effets sur le comportement des individus et leur capacité à survivre et se reproduire, ainsi que sur leur dynamique sociale (ex : mouvements intergroupes des individus, associations entre groupes). Cependant, comme énoncé dans l'introduction, (i) les résultats des études qui se sont intéressées à l'effet de la taille de groupe sur le comportement des individus sont hétérogènes, (ii) l'effet de la taille de groupe sur les paramètres démographiques a été peu étudié en dehors des espèces à reproduction communautaire ou coopérative, (iii) le lien entre le comportement des individus et leur capacité à survivre et se reproduire reste mal compris, et (iv) la relation entre les dynamiques d'associations entre groupes et leurs tailles est peu documentée.

Dans ce contexte, l'objectif de ce travail de thèse était d'étudier l'effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale du zèbre des plaines en contexte de prédation. Pour ce faire, je me suis appuyée sur des données démographiques collectées au sein de deux populations sauvages : celle du Parc de Hluhluwe-iMfolozi (HiP) en Afrique du Sud et celle du Parc National de Hwange (HNP) au Zimbabwe. Dans cette dernière, des données comportementales, GPS et hormonales ont aussi été utilisées.

Résumé des chapitres et résultats

Dans le chapitre 1, je me suis intéressée à l'effet de la taille de groupe sur le comportement des individus et les implications que cela peut avoir sur leur survie. J'ai d'abord étudié la manière dont les zèbres ajustent leur comportement en fonction de la taille du groupe dans lequel ils se trouvent afin de déterminer les coûts et bénéfices comportementaux associés aux différentes tailles de groupe. Pour ce faire, j'ai réalisé quatre sessions de terrain à HNP durant lesquelles j'ai collecté des données comportementales en me focalisant sur quatre comportements : la vigilance individuelle, la vigilance collective, l'acquisition des ressources et les interactions agonistiques. J'ai ensuite utilisé les données démographiques issues du suivi à long terme de la population de zèbres de HNP auxquelles j'ai appliqué des modèles multi-états de Capture-Marquage-Recapture (CMR) et des modèles de Cox afin d'estimer des taux de survie apparente pour les adultes et les poulains appartenant à des harems de tailles différentes. Les résultats obtenus montrent que la probabilité qu'au moins un individu soit vigilant dans le groupe (ce qu'on appelle la vigilance collective ; Lima 1995) augmente avec la taille de groupe, ce qui supporte notre hypothèse de départ. Cependant, de manière inattendue, il apparaît que la taille de groupe n'a pas un effet

systématique sur la vigilance individuelle, et il en est de même pour le lien entre le temps que les individus passent à fourrager et la taille du groupe dans lequel ils se trouvent. Ces résultats, combinés au fait que les interactions agonistiques ont rarement été observées, suggèrent qu'il n'y a pas de coûts associés à la vie en groupe pour les zèbres de HNP, voire qu'il y a certains bénéfices puisque la probabilité d'observer au moins un individu vigilant dans les groupes augmente avec la taille des groupes, ce qui devrait faciliter la vigilance collective. Cependant, ces bénéfices ne semblent pas se traduire par une augmentation de la survie des individus. En combinant des données comportementales et démographiques, cette étude souligne que les effets de dilution et de détection pourraient ne pas toujours avoir d'importance sur le plan comportemental et démographique, et interroge sur la généralité et la systématité de ces effets.

Dans le chapitre 2, je me suis intéressée à l'effet de la taille de groupe et plus particulièrement à l'effet du nombre de femelles reproductrices dans les harems sur la probabilité d'observer un changement d'étalon au sein de ces derniers. Pour cela, j'ai utilisé les données issues du suivi démographique de la population de zèbres de HNP. Les résultats ont montré que les changements d'étalon sont fréquents, et que la probabilité qu'il y ait un changement d'étalon au sein des harems augmente à mesure que le nombre de femelles reproductrices dans les harems augmente. J'ai ensuite combiné ces données démographiques avec des données issues du suivi hormonal des femelles (qui permettent de déterminer le statut de gestation de ces dernières et d'avoir connaissance de la naissance de poulains qui auraient pu ne jamais être observés sur le terrain) pour déterminer si la survie des poulains diminue lorsque l'étalon du harem auquel ils appartiennent change peu de temps avant ou après leur naissance. Cela a permis de tester l'existence du comportement d'infanticide et de déterminer l'importance de celui-ci sur la dynamique des populations de zèbres. Les résultats obtenus montrent que la survie des poulains ne diffère pas significativement entre des situations où l'étalon du harem a été remplacé peu de temps avant ou après leur naissance et des situations où l'étalon n'a pas été remplacé. Cela suggère que, si le comportement d'infanticide par les mâles existe chez le zèbre des plaines en milieu sauvage, il doit être très rare et ne pas avoir de conséquences importantes sur la survie des poulains à l'échelle de la population, qui est un facteur clé sous-tendant la dynamique de cette population (Grange et al. 2015). Cette analyse permet de mieux comprendre le rôle des dynamiques sociales dans la régulation des populations de zèbres des plaines.

Dans le chapitre 3, je me suis ensuite intéressée à la dynamique des formations de troupeaux et à l'effet du nombre de femelles reproductrices dans les harems sur la probabilité pour les harems d'être observés seuls ou en troupeau (avec d'autres harems ou avec des *bachelors*). Pour réaliser cette analyse, j'ai utilisé les données issues des suivis démographiques

des populations de zèbres de HNP et HiP. Les résultats montrent que le nombre de femelles reproductrices au sein des harems a peu d'effet sur la probabilité des harems à être seuls ou en troupeau avec d'autres harems, mais qu'il semble avoir une influence sur la probabilité des harems à s'associer avec des groupes de *bachelors* : les harems comprenant davantage de femelles reproductrices semblent être moins souvent observés avec des groupes de *bachelors* que les plus petits harems (bien que des incertitudes demeurent, notamment à HNP). De plus, les associations entre groupes sont plus fréquentes dans les habitats ouverts, ce qui est particulièrement vrai pour les associations harems-*bachelors* pour lesquelles les habitats ouverts rendent clairement ces associations plus probables. Globalement, les résultats de ce chapitre suggèrent que les harems comprenant un grand nombre de femelles reproductrices pourraient chercher à éviter les groupes de *bachelors*, et semblent d'ailleurs mieux y arriver à HiP où la végétation est globalement plus fermée qu'à HNP. En accord avec cela, les résultats montrent également qu'à HiP la probabilité de changement d'étalon dans les harems n'augmente pas avec le nombre de femelles reproductrices dans les harems, contrairement à ce qui a été observé à HNP. Cette analyse permet d'enrichir notre vision des facteurs déterminant les associations spatiales entre groupes au sein des populations.

Enfin, l'analyse complémentaire et préliminaire a permis de documenter pour la première fois la dynamique des formations de troupeaux (événements de fusion) entre paires de harems (dyades). Pour ce faire, j'ai utilisé les données collectées via des colliers GPS qui ont été déployés sur 34 femelles adultes de différents harems entre 2009 et 2017 dans la population de HNP. Grâce à ces données, j'ai déterminé les événements de fusion entre dyades et j'ai estimé (i) le temps que les dyades passent ensemble, (ii) la fréquence des événements de fusion et la proportion de temps que les dyades passent ensemble en fonction du chevauchement de leurs domaines vitaux et des saisons, (iii) la distance que les dyades parcourent ensemble et la distance à laquelle elles s'éloignent de leur point de rencontre en fonction du temps qu'elles passent ensemble et des saisons, ainsi que (iv) la distribution spatiale et temporelle de ces événements de fusion. Les résultats montrent que les dyades restent en moyenne entre 6 et 7 heures ensemble. Le chevauchement des domaines vitaux n'est pas un fort déterminant de la probabilité des dyades à s'associer et de la proportion de temps qu'elles passent ensemble. En revanche, les événements de fusion sont plus fréquents et les dyades passent une plus grande proportion de leur temps ensemble en saison des pluies qu'en saison sèche. De plus, lorsque la ressource en eau se fait rare, les localisations où les dyades sont ensemble sont enregistrées plus proches des points d'eau pompés que les localisations où les dyades ne sont pas ensemble. Enfin, les paires de harems semblent s'associer lorsque le risque de prédation est plus élevé (nuit, aube et crépuscule). Cette

analyse préliminaire améliore nos connaissances sur la dynamique des associations entre harems au sein des sociétés multi-niveaux de zèbres des plaines.

Pour résumer, ce travail de thèse a contribué à améliorer nos connaissances sur l'effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale du zèbre des plaines, une espèce qui vit dans des groupes stables et dont la reproduction n'est ni communautaire, ni coopérative. Au vu des résultats présentés dans ce manuscrit, il apparaît que la taille de groupe a peu d'effet sur la plupart des comportements étudiés (vigilance individuelle, acquisition des ressources) et n'a pas d'effet significatif sur la survie des individus (chapitre 1). En revanche, la taille de groupe a un effet sur la probabilité de changement d'étalon dans les harems puisque cette probabilité est positivement corrélée au nombre de femelles reproductrices présentes dans les harems à HNP (chapitre 2). De plus, il apparaît que ces changements d'étalon liés à la taille de groupe n'affectent pas significativement la survie des poulains à HNP (chapitre 2). La taille de groupe semble aussi avoir un effet sur la dynamique des formations de troupeaux, particulièrement sur les associations harems-*bachelors* : les harems comprenant davantage de femelles reproductrices sont moins souvent observés en troupeau avec des *bachelors* (chapitre 3). Les grands harems semblent donc éviter les *bachelors* et réussissent mieux à le faire à HiP où la végétation est globalement plus fermée qu'à HNP. En accord avec cela, il apparaît que la probabilité de changement d'étalon au sein des harems n'augmente pas avec le nombre de femelles reproductrices dans les harems à HiP (chapitre 3). Enfin, ce travail de thèse a permis d'accroître nos connaissances sur la dynamique des associations entre harems au sein des sociétés multi-niveaux de zèbres des plaines (analyse complémentaire et préliminaire).

LIMITATIONS

Effet de la taille de groupe sur les paramètres démographiques des individus partiellement étudié

Dans ce travail de thèse, les analyses se sont focalisées sur l'effet de la taille de groupe sur la survie des adultes et des poulains puisque l'objectif était de faire le lien entre (i) le comportement des individus et leur survie (chapitre 1), et (ii) les changements d'étalon dans les harems (dont la probabilité est positivement corrélée au nombre de femelles reproductrices à HNP) et la survie des poulains (chapitre 2). L'effet de la taille de groupe sur les paramètres démographiques des individus a donc été partiellement exploré puisque le lien entre taille de groupe et succès reproducteur des individus n'a pas été étudié. Les individus appartenant à de grands groupes pourraient avoir un meilleur succès reproducteur si la sécurité accrue dont ils sont censés

bénéficier leur permet de réduire le temps qu'ils dédient au comportement de vigilance et d'augmenter le temps qu'ils consacrent à s'alimenter (*group size effect on vigilance*; Elgar 1989, Lima 1995, Roberts 1996, Beauchamp 2008) ce qui pourrait conduire à une augmentation de leur condition corporelle. Les individus en bonne condition pourraient alors consacrer une part plus importante de leurs réserves énergétiques pour leur reproduction (Atkinson and Ramsay 1995, Côté and Festa-Bianchet 2001). Des études ont notamment montré un effet positif de la condition corporelle des femelles sur les taux de natalité (Testa and Adams 1998, Campbell and Gerald 2004). Cependant, les résultats obtenus dans le chapitre 1 suggèrent que cette hypothèse est peu probable chez les zèbres des plaines de HNP étant donné que (i) le temps que les zèbres passent à fourrager ne semble pas être positivement corrélé à la taille du groupe dans lequel ils se trouvent, et que (ii) 90% des *bouts* (périodes) de vigilance qui ont été enregistrés sont des *bouts* où les zèbres mâchent de la nourriture tout en étant vigilant, ce qui suggère que les individus n'ont pas de compromis à faire entre vigilance et alimentation la plupart du temps. Les individus appartenant à de grands groupes pourraient également bénéficier d'une meilleure acquisition des ressources si ces derniers ont plus de chance de supplanter d'autres groupes et d'avoir accès à des patches de ressources alimentaires convoités, comme cela a été montré chez plusieurs espèces (Cassidy et al. 2015, Majolo et al. 2020 ; mais voir Roth and Cords 2016, Jordan et al. 2017). A Hwange, cette hypothèse est peu probable puisqu'il a été montré que les zèbres des plaines sont principalement limités par la prédation, et non par les ressources alimentaires (Grange and Duncan 2006, Grange et al. 2015).

De plus, il est important de noter que le fait d'avoir étudié l'effet de la taille de groupe sur la survie des poulains, de manière directe dans le chapitre 1 et de manière indirecte dans le chapitre 2 (via l'effet des changements d'étalon dont la probabilité est positivement corrélée au nombre de femelles reproductrices dans les harems à HNP) permet d'avoir une vision partielle de l'effet que peut avoir la taille de groupe sur le succès reproducteur des individus. En effet, la survie juvénile est l'une des mesures du succès reproducteur et est souvent le facteur qui influe le plus la dynamique des populations d'ongulés du fait de sa variabilité (Gaillard et al. 1998, 2000).

Peu de populations étudiées

Dans le cadre de ma thèse, je me suis focalisée sur deux populations de zèbres des plaines uniquement. Les résultats des chapitres 2 et 3 ont souligné des différences entre ces deux populations au niveau de la relation entre le nombre de femelles reproductrices dans les harems et (i) la probabilité de changement d'étalon, et (ii) la probabilité pour les harems d'être observés seuls ou en troupeau, ce qui suggère de ne pas généraliser les résultats de cette thèse. En effet, la


structure de l'habitat, la densité de prédateurs, et la densité de conspécifiques et de partenaires de dilution (autre espèce qui partage un prédateur en commun, Schmitt et al. 2014) sont autant de facteurs pouvant varier entre populations et moduler l'effet de la taille de groupe sur le comportement des individus, leur survie et leur reproduction, et les dynamiques d'associations entre groupes. La structure des habitats (ouverture, fragmentation) peut moduler la dynamique des interactions sociales entre individus ou entre groupes en affectant la fréquence à laquelle ces interactions ont lieu (He et al. 2020). Par exemple, chez le scinque rugueux *Tiliqua rugosa*, Leu et al. (2016) ont mis en évidence que les interactions entre individus étaient plus fréquentes et les réseaux sociaux plus denses dans les habitats comprenant des barrières qui contraignent le mouvement des individus. Chez les zèbres des plaines, les résultats du chapitre 3 ont montré que la probabilité d'observer des harems en troupeaux augmentait avec l'ouverture de l'habitat. En modifiant la structure sociale des populations, l'ouverture et la fragmentation des habitats peuvent avoir des conséquences sur les paramètres démographiques des individus, via des effets sur le risque de prédation (Rubenstein 1986, Schreier and Swedell 2009, Tong et al. 2015, Lin et al. 2020), la transmission de parasites (Godfrey et al. 2009, Vander Wal et al. 2012, MacIntosh et al. 2012), le transfert d'information sur la localisation de patches de ressources (Aplin et al. 2012) ou la coopération (Voelkl and Kasper 2009, Wu et al. 2010) par exemple. La densité de prédateur peut aussi modifier l'effet qu'a la taille de groupe sur le comportement des individus. Des études ont mis en évidence des effets de la présence des prédateurs dans l'habitat (périodes risquées) et du type d'habitat (zones risquées) sur la distribution spatiale des ongulés (Creel and Winnie 2005, Valeix et al. 2009, Thaker et al. 2011), leur comportement de vigilance et d'alimentation (Winnie and Creel 2007, Creel et al. 2014) et leur dynamique d'agrégation avec d'autres groupes (Creel and Winnie 2005). Ces facteurs pourraient se confondre avec l'effet de la taille de groupe et le masquer : au sein de populations faisant face à une forte densité de prédateurs, la diminution attendue de la vigilance individuelle avec la taille de groupe pourrait être moins marquée du fait du risque accru de prédation auquel les individus sont exposés, ce qui pourrait contraindre ces derniers à maintenir un niveau de vigilance élevé même au sein de grands groupes. L'effet de la densité de prédateurs pourrait être un modulateur particulièrement important de l'effet taille de groupe chez le zèbre des plaines puisque cette espèce est fortement influencée par la prédation par les lions (Grange and Duncan 2006). Cependant, les proies ne considèrent pas uniquement la densité de prédateurs et les indices visuels, auditifs ou chimiques présents après une attaque d'un prédateur sur une proie (indices de prédation) pour estimer leur risque de prédation, mais également la densité de conspécifiques (hypothèse de *risk-assessment*, Peacor 2003). Dans des populations où la densité de conspécifiques ou de partenaires de dilution est forte, la force de

l'effet de dilution pourrait être plus élevée et de ce fait, la diminution de la vigilance individuelle avec la taille de groupe pourrait être moins marquée.

Les facteurs énoncés précédemment sont susceptibles de différer entre populations et de moduler l'effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale des espèces. Cela souligne l'importance de mener des études comparatives entre populations afin de mieux comprendre le rôle modulateur de ces facteurs sur l'effet de la taille de groupe. Au cours de ma thèse, j'ai tenté de développer une approche de ce type : j'ai mené des prospections dans plusieurs sites qui variaient en termes de pression de prédation afin de déterminer dans quelle mesure la taille des harems et le taux de recrutement au sein de ces derniers (nombre de poulains dans les harems) changent avec le risque de prédation (Box. 1), mais la végétation trop dense durant la période de prospection n'a pas permis d'obtenir suffisamment de données pour conduire une analyse des résultats.

Box 1. Exemple d'une étude multi-population visant à déterminer dans quelle mesure la taille des harems et le taux de recrutement au sein de ces derniers changent avec le risque de prédation

Pendant ma thèse, j'ai tenté de développer une approche comparative, l'idée étant d'étudier une population de zèbres des plaines sans prédateurs de manière similaire à ce que j'ai réalisé sur la zone de *Main Camp* dans le Parc National de Hwange, où les prédateurs sont présents en forte densité. Le Parc National des Matopos, à environ 350 km au



Groupe de zèbres des plaines dans une végétation dense à ZNP

sud de Hwange offrait cette opportunité mais la végétation trop dense en cette période de l'année (la prospection a été réalisée en saison des pluies) n'a pas permis d'obtenir suffisamment de données. Par conséquent, j'ai réalisé des prospections dans d'autres zones du pays où le paysage plus ouvert devait offrir une meilleure visibilité pour observer les zèbres à distance : le Parc National de Kazuma Pan (KNP) et le Parc National du Zambèze (ZNP). Cependant, lors de mes prospections, aucun zèbre n'a été vu dans le Parc National de Kazuma Pan, et seulement trois groupes ont été vus dans le Parc National du Zambèze. La faible taille d'échantillon obtenu n'ayant pas permis de conduire une analyse des résultats, l'effet du risque de prédation sur la taille des harems et le taux de recrutement au sein de ces derniers n'a pas pu être évalué. Néanmoins, cette étude est un bon exemple de recherche qui, en comparant des populations qui diffèrent en termes de risque de prédation par exemple, permettrait d'identifier les facteurs les plus susceptibles de faire varier l'effet de la taille de groupe sur le comportement et les paramètres démographiques des individus, et donc ceux qu'il serait important de mesurer et de considérer dans de futurs travaux de recherche similaires à ceux conduits dans le cadre de cette thèse.

Effet de la composition des groupes partiellement exploré

Cette thèse s'est focalisée sur l'effet de la taille de groupe mais la composition des groupes (autre composant de la socialité) peut aussi avoir d'importants effets sur le comportement des individus, leur capacité à survivre et se reproduire et sur les mouvements intergroupes des individus et les associations entre groupes. En effet, chaque groupe est composé d'individus qui diffèrent de par leur âge et leur sexe, mais aussi de par leur statut de dominance, leurs préférences sociales, leur personnalité, leur sensibilité aux risques et leur expérience, autant d'aspects qui n'ont pas été considérés dans cette thèse bien qu'ils puissent modifier la force des effets de dilution et de détection. Par exemple, les groupes comprenant des juvéniles pourraient davantage s'associer entre eux afin de diluer le risque de prédation accru encouru par les jeunes. Chez le zèbre des plaines, Rubenstein (2010) a montré que le pourcentage de harems comprenant des femelles allaitantes dans les troupes augmente à mesure que le risque de prédation augmente, suggérant un bénéfice pour les femelles en lactation à s'agréger avec d'autres harems composés de femelles allaitantes afin de réduire le risque de prédation pour leurs petits, qui sont plus susceptibles d'être attaqués par les lions (Stander 1992, Mills and Shenk 1992). La présence de juvéniles au sein des groupes pourrait aussi modifier la manière dont les groupes utilisent leur habitat : chez le bouquetin des Alpes *Capra ibex*, la présence des jeunes influence le comportement spatial des mères, ces dernières utilisant plus fréquemment les zones de refuges que les autres femelles (Grignolio et al. 2007). Ainsi, les groupes comprenant des jeunes pourraient sélectionner des zones moins risquées en termes de prédation. Également, si des individus sont apparentés, ils pourraient davantage s'associer avec d'autres individus avec qui ils partagent un lien de parenté, comme cela a été montré chez la girafe (Carter et al. 2013). Chez les zèbres des plaines, Tong et al. (2015) ont mis en évidence que l'apparentement entre les femelles au sein des troupes était plus élevé que par hasard, suggérant un rôle des liens de parenté entre femelles dans la formation des troupes. De plus, indépendamment de leur taille, des groupes comprenant des individus expérimentés pourraient être plus efficaces à trouver de la nourriture (Smith and Metcalfe 1997, Reeb 2000) ou à estimer le risque de prédation auquel ils sont exposés (Fraker 2009, Andreasson et al. 2019), ce qui pourrait procurer des bénéfices en termes de survie et de reproduction à tous les individus du groupe.

Cependant, il est important de noter que la variabilité interindividuelle des zèbres n'a pas été complètement omise dans les travaux présentés dans cette thèse puisque les analyses du chapitre 1 ont pris en compte le sexe, l'âge et le statut reproducteur des individus pour étudier l'effet de la taille de groupe sur leur comportement et leur survie. De plus, les analyses conduites dans les chapitres 2 et 3 ont testé l'effet du nombre de femelles reproductrices dans les harems,

plutôt que celui de la taille des groupes, sur la probabilité de changement d'étalon au sein des harems et sur la probabilité pour les harems d'être observés seuls ou en troupeau.

IMPLICATIONS ET PERSPECTIVES

Ce travail de thèse souligne deux points importants dont je souhaiterais développer les implications et les perspectives dans la suite de cette discussion : le fonctionnement de l'effet de dilution et l'importance des dynamiques sociales dans la régulation des populations.

Le fonctionnement de l'effet de dilution

Les résultats du chapitre 1 suggèrent que l'effet de dilution importe peu sur le plan comportemental et démographique chez le zèbre des plaines. Les résultats obtenus ont en effet montré que la vigilance individuelle ne diminue pas systématiquement avec la taille des groupes et que la taille des harems n'a pas d'effet sur la survie des adultes et des poulains. Cette étude s'ajoute ainsi au nombre croissant de travaux de recherche qui ont montré une absence d'effet de la taille de groupe sur le niveau de vigilance des individus ou des formes inattendues de cette relation (Treves 2000, Laundre et al. 2001, Beauchamp 2008, Périquet et al. 2017, Liu et al. 2020, Luo et al. 2020), ce qui pose la question suivante : l'effet de dilution est-il un phénomène général et systématique ?

Dans le chapitre 1, plusieurs hypothèses pour expliquer l'absence d'effet de la taille de groupe sur la vigilance individuelle des zèbres ont été abordées : l'effet de dilution pourrait ne pas fonctionner si le taux d'attaque augmente avec la taille des groupes, ou bien si les prédateurs attaquent préférentiellement certains individus du groupe. Une autre hypothèse qui a été énoncée brièvement dans ce chapitre est que l'effet de dilution pourrait agir à une échelle supérieure que celle du groupe. Je souhaiterais ici développer ce point plus en détail.

L'effet de dilution est un effet numérique immédiat qui prédit que chaque membre d'un groupe verra sa probabilité d'être ciblé par le prédateur (et donc son risque de prédation) diminuer lorsque la taille du groupe augmente (Bertram 1978, Turner and Pitcher 1986, Lehtonen and Jaatinen 2016). Cet effet fonctionne à condition que le prédateur ne puisse prélever qu'une seule proie à la fois et que le taux d'attaque n'augmente pas avec la taille du groupe de proies. Lors d'une attaque, chaque individu a donc une probabilité de $1/N$ d'être sélectionné par le prédateur, N étant le nombre total d'individus dans le groupe. De manière logique, le risque de prédation pour chaque individu diminue donc à mesure que le nombre d'individus dans le groupe augmente, et de par cette sécurité accrue, on s'attend à observer une diminution de la vigilance

individuelle et une augmentation de la survie des individus à mesure que la taille de groupe augmente. Cependant, toutes les études qui se sont intéressées à l'effet de dilution ont été conduites à l'échelle du groupe ou du troupeau (ex : Childress and Lung 2003, Ebensperger et al. 2006, Périquet et al. 2010, Creel et al. 2014, Wang et al. 2015, van der Marel et al. 2019, Liu et al. 2020 ; voir aussi références dans Treves 2000, Beauchamp 2008). Or, il me semble important de souligner que l'effet de dilution pourrait aussi fonctionner à une échelle plus large. En effet, si un prédateur attaque un groupe de proies, le risque de prédation pourrait être dilué pour les autres groupes présents dans la zone de recherche de nourriture du prédateur. Dans ce contexte, ce sont tous les individus présents dans cette zone, et non plus seulement les membres du groupe, qui diluent le risque de prédation. Cet effet de dilution à grande échelle pourrait se mettre en place fréquemment chez les espèces dont les groupes partagent le même espace et se retrouvent souvent dans le même patch de recherche de nourriture d'un prédateur, et pourrait fonctionner même si ces groupes sont à plusieurs kilomètres les uns des autres. A noter cependant que si les groupes sont éloignés les uns des autres, l'effet de dilution pourrait ne pas nécessairement conduire à une diminution de la vigilance individuelle avec la taille de groupe. En effet, il est possible que les individus d'un groupe n'ajustent pas leur niveau de vigilance en fonction du nombre réel de conspécifiques présents dans le patch de ressources du prédateur puisqu'ils sont à distance et ne les perçoivent pas, mais plutôt en fonction du nombre perçu, c'est-à-dire le nombre d'individus présents dans le groupe ou à proximité du groupe (échelle du troupeau). Néanmoins, l'effet de dilution devrait conduire à une augmentation de la survie des individus, puisque, même si les groupes de proies présents dans la zone ne se perçoivent pas, l'attaque d'un prédateur sur l'un de ces groupes devrait procurer des bénéfices directs aux autres groupes en termes de survie.

Tester l'effet de dilution au-delà de l'échelle du groupe me semble un angle d'approche intéressant pour mieux comprendre le fonctionnement de cet effet. Les futures recherches qui s'intéresseront à tester l'effet de dilution pourraient considérer des échelles plus grandes que celle du groupe ou du troupeau, en prenant en compte le nombre total d'individus présents à l'échelle du patch de recherche de nourriture du prédateur plutôt que se limiter au nombre d'individus présents dans un rayon de largeur arbitraire, comme cela est souvent le cas (ex : Childress and Lung 2003, Winnie and Creel 2007, Shi et al. 2010, Li et al. 2012, Pays et al. 2014, Wang et al. 2015, Liu et al. 2020, chapitre 1 de cette thèse). Il peut aussi être intéressant de prendre en compte la présence dans l'environnement des partenaires de dilution, puisque ces derniers peuvent diluer le risque de prédation pour l'espèce étudiée. De nombreuses espèces s'associent fréquemment en groupes multi-espèces, comme c'est le cas chez les ongulés par

exemple (Leuthold 1977, Fitzgibbon 1990, Schmitt et al. 2014, Pays et al. 2014), et plusieurs études ont mis en évidence que la présence d'individus hétérospécifiques partageant un même prédateur à proximité d'un groupe diminue le niveau de vigilance des individus du groupe, notamment chez les primates non humains (Cords 1990, Chapman and Chapman 1996), les oiseaux (Metcalf 1984, Popp 1988, Sridhar et al. 2009) et les ongulés (Périquet et al. 2010, Schmitt et al. 2014, 2016, Creel et al. 2014, Stears et al. 2020 ; mais voir Fitzgibbon 1990, Pays et al. 2014). Les espèces qui jouent le rôle de partenaires de dilution devraient aussi être prises en compte, puisque plusieurs études ont montré que certaines espèces de proies sont préférentiellement ciblées par les prédateurs (Sinclair et al. 2003, Hayward and Kerley 2005), ce qui pourrait augmenter leur force de dilution (Fitzgibbon 1990). La force de l'effet de dilution pourrait donc être plus ou moins forte en fonction du cortège d'espèces présentes à proximité du groupe étudié.

Développer un modèle qui permettrait d'étudier le fonctionnement de l'effet de dilution dans un environnement plus complexe que la vision généralement supposée (c.-à-d. un seul groupe ou troupeau de proies attaqué par un prédateur sans prise en compte de l'environnement complexe qui entoure le groupe) serait aussi pertinent. Récemment, Patin et al. (2019) ont développé un modèle pour mieux comprendre les interactions entre taille de groupe, vigilance et utilisation de l'espace chez le zèbre des plaines : ce modèle a permis de déterminer la vigilance et l'utilisation de l'espace optimales pour des individus solitaires et pour des individus meneurs et suiveurs dans des groupes de différentes tailles. Les résultats de cette étude ont mis en évidence que les attentes quant à la forme et la force de la relation entre vigilance individuelle et taille de groupe sont complexes et sensibles à la manière dont la vigilance et l'utilisation de l'espace affectent l'acquisition des ressources alimentaires et le risque de prédation. Ce modèle pourrait être un point de départ possible pour, ici, modéliser le risque de prédation encouru par chaque proie dans diverses situations plus ou moins complexes. Cela permettrait de déterminer comment le risque de prédation d'un individu est modulé par le nombre de groupes de proies présents dans le patch de recherche de nourriture du prédateur par exemple. Il serait aussi possible de tester si la présence de groupes de conspécifiques produit un effet de dilution plus fort que la présence de groupes hétérospécifiques partageant le même prédateur. Ce modèle pourrait être appliqué à des habitats plus ou moins complexes, variant en termes de structure d'habitat pour tester si la perception visuelle entre groupes de proies est un modulateur de l'effet de dilution, ou en termes de densité de prédateur pour voir si la présence de plusieurs prédateurs module l'effet de dilution. En considérant l'effet de dilution à une échelle plus large, cela permettrait de

comprendre la relation complexe qui existe entre taille de groupe et vigilance, et permettrait d'établir les conditions dans lesquelles l'effet de dilution au sein d'un groupe peut se produire.

L'importance des dynamiques sociales dans la régulation des populations

Il est de plus en plus reconnu que les interactions sociales entre individus et entre groupes peuvent affecter la survie et la reproduction des individus. En effet, de nombreuses études ont mis en évidence des effets bénéfiques des interactions sociales sur la survie et le succès reproducteur des individus chez plusieurs espèces (marmotte à ventre jaune *Marmota flaviventris* : Blumstein et al. 2018 ; cheval sauvage *Equus ferus* : Cameron et al. 2009 ; babouin jaune *Papio cynocephalus* : Silk et al. 2003 ; suricate *Suricata suricatta* : Newman et al. 2016 ; souris gris *Mus musculus* : Weidt et al. 2008). Les interactions sociales peuvent aussi être bénéfiques en termes de protection contre le risque d'infanticide (Palombit 1999; mais voir Kalbitzer et al. 2017), de réduction du stress (Wittig et al. 2016) ou de diminution du risque de harcèlement des femelles par des *bachelors* (Linklater et al. 1999, Sundaresan et al. 2007).

Les analyses de réseaux sociaux, en mesurant la connexion des individus au sein des populations, sont un outil utile pour déterminer le nombre de relations sociales entretenues par chaque individu mais également la force de ces interactions et la position des individus au sein de ces réseaux (Farine and Whitehead 2015), des facteurs qui peuvent avoir un effet bénéfique sur leur survie et leur succès reproducteur (Ryder et al. 2009, Oh and Badyaev 2010, Montero et al. 2020). Chez les espèces vivant dans des sociétés multi-niveaux, les analyses de réseaux sociaux peuvent être conduites à l'échelle du groupe afin de déterminer le degré de « socialité » de chaque groupe et offre la possibilité de tester des hypothèses sur le lien entre la taille des groupes, le nombre d'interactions sociales qu'ils entretiennent et les paramètres démographiques des individus qui les constituent (Box.2).

Box 2. Analyse de réseaux sociaux dans les sociétés multi-niveaux

Dans le cadre de ma thèse, j'ai conduit une analyse exploratoire dont l'objectif était de déterminer si la taille des harems était corrélée à leur taux d'association avec d'autres groupes (harems et *bachelors*). En utilisant les données issues du suivi démographique de la population de zèbres des plaines de HiP qui indiquent pour chaque observation d'un harem si ce dernier était seul ou en troupeau avec d'autres groupes (et si oui, lesquels), les valeurs



de degré pondéré (*weighted degree*) ont été calculées pour des harems de tailles différentes (N = 69). La valeur de degré pondéré est une mesure qui représente les interactions totales attendues (ou taux d'association) pour chaque harem. Ainsi, pour un harem avec une valeur de degré pondéré de 2, on s'attend à ce que ce harem soit observé avec 2 autres groupes en moyenne. Les résultats de cette analyse exploratoire montrent que les petits harems semblent être davantage connectés à d'autres groupes que les harems de moyenne et grande tailles (Fig. 1). Par la suite, il serait intéressant d'estimer la survie apparente des individus au sein de ces groupes pour tester si les individus appartenant à des groupes plus fortement connectés socialement au sein de la population bénéficient d'un avantage en termes de survie.

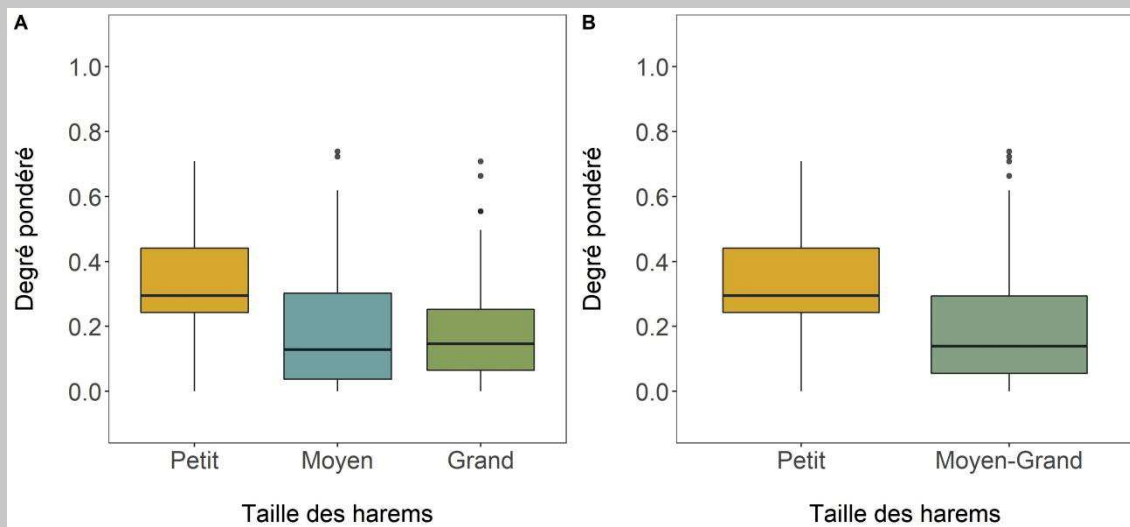


Figure 1. Relation entre valeurs de degré pondéré et tailles des harems, distribuées en 3 classes (A) et 2 classes (B). Les harems de petite taille comprennent entre 2 et 3 individus, les harems de taille moyenne comprennent entre 4 et 5 individus, et les harems de grande taille comprennent 6 individus et plus.

Comme les interactions sociales entre individus et groupes sont associées à des coûts et bénéfiques, celles-ci pourraient avoir un effet régulateur sur la dynamique sociale des espèces en modulant les associations entre groupes. En effet, de même que la ségrégation sexuelle (le fait que les femelles et mâles adultes vivent en groupes distincts) est expliquée par des différences sexuelles de sélection alimentaire, de stratégie de reproduction, de préférences sociales et/ou de

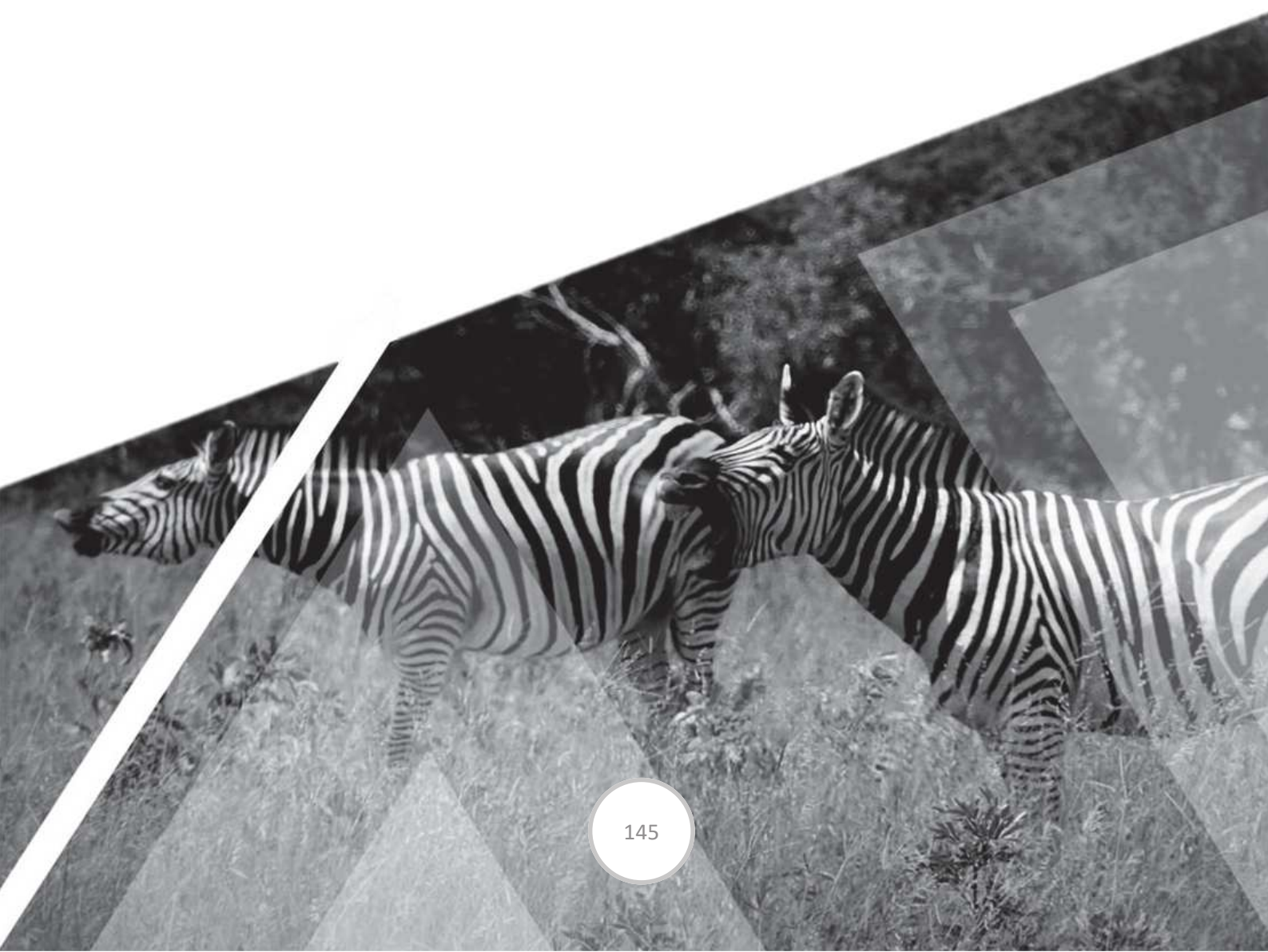
rythmes d'activité distincts (Ruckstuhl and Neuhaus 2006), la distribution spatiale des groupes sociaux pourrait être expliquée par des différences en termes de coûts et bénéfices liés à leur taille et leur composition respectives. Par exemple, comme nous l'avons vu dans cette thèse, des groupes comprenant un grand nombre de femelles reproductrices pourraient être des cibles préférentielles pour les *bachelors*, ce qui pourrait augmenter le risque de changement de mâle et de harcèlement des femelles pour ces groupes (chapitre 2). Ces groupes pourraient alors éviter de s'associer avec les groupes de *bachelors* afin de réduire la menace que ces derniers représentent (chapitre 3). Chez le gelada *Theropithecus gelada*, Pappano et al. (2012) ont montré que les *bachelors*, en tant que prédateurs « sociaux » avaient un rôle important sur le comportement spatial des groupes reproducteurs : ces groupes se rassemblent et réduisent la distance qui les sépare lorsque des *bachelors* sont en approche. À terme, cela peut modifier leur utilisation de l'espace en réduisant potentiellement leur accès à des zones refuges ou à des patchs où les ressources sont abondantes et/ou de bonne qualité, si ces prédateurs « sociaux » y sont présents. Chez les espèces chez lesquelles les conflits intergroupes peuvent avoir des conséquences létales, les groupes évitent les endroits où le risque de rencontrer d'autres groupes est plus élevé (*risk hypothesis*, Wrangham et al. 2007), générant ainsi une hétérogénéité spatiale au sein du paysage de la peur, au même titre que le risque de prédation (Willems and Hill 2009, Laundre et al. 2010). Récemment, Tórriz-Herrera et al. (2020) ont montré que les groupes de capucins à face blanche du Panama *Cebus capucinus* sous-utilisent les zones où leurs domaines vitaux se chevauchent avec ceux d'autres groupes, qui sont des zones qu'ils perçoivent comme dangereuses, soulignant ainsi le rôle des interactions sociales entre groupes sur l'utilisation de l'espace de ces derniers.

Dans ce contexte, il se pose alors la question de savoir comment les groupes gèrent ces dynamiques sociales dans un environnement complexe. En effet, les groupes pourraient avoir peu d'information sur la localisation des groupes de conspécifiques avec qui ils pourraient s'associer et ceux qu'ils doivent essayer d'éviter. Il est possible cependant que la distribution spatiale des groupes de conspécifiques soit plus facile à prévoir que la localisation des prédateurs puisque les individus conspécifiques partagent les mêmes prédateurs et les mêmes ressources et il est donc probable qu'ils se retrouvent ensemble dans des patchs qui leur sont favorables. Comme abordé dans le chapitre 3 de cette thèse, l'environnement pourrait jouer un rôle dans cette dynamique sociale : percevoir et choisir de s'associer ou d'éviter des groupes pourrait être plus facile dans les habitats ouverts qui permettent de percevoir les autres groupes à distance (Gerard et al. 1993, Gerard and Loisel 1995, Pays et al. 2007a, Isvaran 2007, Fortin et al. 2009).

Globalement, cela souligne la complexité des facteurs qui modulent l'utilisation de l'espace par les groupes de proies où la prédation et la distribution des ressources, mais aussi les

interactions sociales entre individus et entre groupes, agissent ensemble et modifient la distribution spatiale des groupes. La vie en groupe confère des bénéfices et des coûts, ce qui implique que les groupes doivent en permanence faire des compromis entre trouver suffisamment de ressources (nourriture, eau) pour combler leurs besoins nutritionnels, mais aussi diminuer leur risque de prédation et s'associer avec des groupes qui ne représentent pas de menace pour eux (conflit pour avoir accès aux ressources, harcèlement des femelles, infanticide), et ajuster leur utilisation de l'espace en conséquence. Une perspective envisageable serait de développer un modèle qui permettrait de simuler le comportement spatial des groupes dans des environnements complexes où chaque groupe déciderait à chaque pas de temps du patch vers lequel aller, chaque patch variant en termes de risque de prédation, de qualité et d'abondance des ressources alimentaires, de structure de l'habitat, et de présence de prédateurs « sociaux » et de partenaires de dilution. En étudiant comment ces facteurs (risque de prédation, distribution des ressources, associations entre groupes) interagissent ensemble et contribuent à déterminer l'utilisation de l'espace par les groupes sociaux au sein des populations, cette approche de modélisation permettrait d'offrir un aperçu théorique sur cette question.

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ABSTRACT

In social species, costs and benefits of group living are numerous and dynamic, and the balance between them is a key determinant of group size. Group size is a component of sociality which can have important effects on the behaviour of individuals, their demographic parameters and their social dynamic (intergroup movements of individuals, associations between groups). However, these effects remain poorly understood. In this thesis, I explore the effect of group size on the behaviour, demography and social dynamic of plains zebras *Equus quagga* in the wild populations of Hwange National Park (HNP, Zimbabwe) and Hluhluwe-iMfolozi Park (HiP, South Africa). In the first chapter, I show that, in HNP, group size has little effect on individual vigilance and foraging, and has no significant effect on the survival of individuals, suggesting that dilution and detection effects do not matter behaviourally and demographically in this population. In the second chapter, I show that the probability of stallion turnover increases with the number of reproductive females in harems in HNP, but that these stallion turnovers do not affect foal survival. This suggests that, if infanticide by males occurs in wild plains zebras, this should be extremely rare and has no important consequences for foal survival at the population level. Finally, in the third chapter, I show that the number of reproductive females in harems has no effect on the probability for harems to be alone or with other harems. However, harems with many reproductive females seem to be found less often near bachelors (although significant uncertainty remains). This suggests that harems including many reproductive females may seek to avoid bachelors, and actually seem to have more success in doing it in HiP where vegetation is overall more closed than in HNP. Accordingly, the probability of stallion turnover does not increase with the number of reproductive females in harems in HiP. Overall, this thesis questions the functioning of the dilution effect and highlights the importance of considering the potential regulatory effect of social dynamics on populations, through their effect on the spatial distribution of groups.

KEYWORDS: sociality, behaviour, demography, social dynamic, ungulate, predation

RESUME

Chez les espèces sociales, les coûts et bénéfices de la vie en groupe sont nombreux et dynamiques, et la balance entre ces derniers est un déterminant clé de la taille des groupes. La taille de groupe est un composant de la socialité qui peut avoir d'importants effets sur le comportement des individus, leurs paramètres démographiques et leur dynamique sociale (mouvements intergroupes des individus, associations entre groupes). Cependant, ces effets restent mal compris. Dans cette thèse, j'explore l'effet de la taille de groupe sur le comportement, la démographie et la dynamique sociale du zèbre des plaines *Equus quagga* dans les populations sauvages du Parc National de Hwange (HNP, Zimbabwe) et du Parc de Hluhluwe-iMfolozi (HiP, Afrique du Sud). Dans le premier chapitre, je montre qu'à HNP la taille de groupe a peu d'effet sur la vigilance individuelle et l'acquisition des ressources, et n'a pas d'effet significatif sur la survie des individus, ce qui suggère que les effets de dilution et de détection importent peu sur le plan comportemental et démographique dans cette population. Dans le second chapitre, je montre que la probabilité qu'il y ait un changement d'étalon au sein des harems augmente lorsque le nombre de femelles reproductrices dans les harems augmente à HNP, mais que ces changements d'étalon n'affectent pas la survie des poulains. Ainsi, si le comportement d'infanticide par les mâles existe chez le zèbre des plaines en milieu sauvage, il devrait être très rare et ne pas avoir d'impact important sur la survie des poulains à l'échelle de la population. Enfin, dans le troisième chapitre, je montre que le nombre de femelles reproductrices dans les harems n'a pas d'effet sur la probabilité des harems à être observés seuls ou avec d'autres harems. En revanche, les harems comprenant davantage de femelles reproductrices semblent être moins souvent observés avec des groupes de mâles célibataires (bien que des incertitudes demeurent). Cela suggère que les harems comprenant beaucoup de femelles reproductrices pourraient éviter de s'associer avec les mâles célibataires, et semblent mieux réussir à les éviter à HiP où la végétation est globalement plus fermée qu'à HNP. De ce fait, la probabilité qu'il y ait un changement d'étalon au sein des harems n'augmente pas avec le nombre de femelles reproductrices dans les harems à HiP. Globalement, cette thèse remet en question le fonctionnement de l'effet de dilution et souligne l'importance de considérer l'effet régulateur potentiel des dynamiques sociales sur les populations, à travers leur effet sur la distribution spatiale des groupes.

MOTS CLÉS : socialité, comportement, démographie, dynamique sociale, ongulé, prédation