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le 20 Avril 2017

**Mouvements collectifs et structure sociale chez le
zebrafish en environnement fragmenté**

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Résumé

La prise de décision collective est un des mécanismes utilisés par les espèces sociales lors d'événements de collectes de nourriture, d'optimisation de chemins, de mouvements collectifs, de fuites face à un prédateur ou bien même de sélections d'habitat. Les zebrafish (*Danio rerio*), animaux grégaires de référence en biologie, n'ont jamais été étudiés dans des contextes de choix collectifs binaires et il nous semblait légitime d'analyser leurs comportements décisionnels. L'objectif de cette thèse est de répondre aux attentes du projet ASSISI de création d'un système expérimental modulable capable d'accueillir robots comme poissons, de mise au point d'une société mixte adaptative auto-organisée, et de caractérisation des comportements individuels et collectifs des zebrafish implémentables dans les robots.

Nos observations montrent que la prise collective de décision et la cohésion des groupes en environnement ouvert, et présentant deux points de repère identiques, sont des processus dynamiques qui varient selon la souche de *Danio rerio* (AB ou TL) et sont liées à la densité des populations. Constamment en mouvement, les poissons oscillent entre les deux points de repère identiques installés dans leur environnement. La souche AB est toujours plus attirée par ces hétérogénéités et est beaucoup moins cohésive que la souche TL.

En environnement contraint, de type deux chambres reliées par un couloir, nous réitérons le même type d'expérience chez la souche la plus à même de prendre des décisions collectivement (AB) et en faisant varier la densité des groupes de 1 à 20 individus. Il ressort que les *Danio rerio* de type AB restent essentiellement en groupe mais que l'augmentation de leur densité tend à les diviser. Nous remarquons aussi que la densité influe partiellement sur la topologie du groupe : il existe, lors des sorties collectives, une corrélation entre l'ordre de sortie des zebrafish (les suiveurs) et l'ordre de distance de chaque individu par rapport à l'initiateur des dites sorties. Cette corrélation est d'autant plus forte quand les suiveurs sont soit très proches, soit les plus éloignés de l'initiateur.

Le dispositif expérimental précédent nous permet d'autre part de nous concentrer sur la notion de leadership chez des groupes de 2 à 10 *Danio rerio* AB. Nous mettons en évidence que chaque poisson initie au moins une fois un départ collectif, le nombre d'initiations effectives est proportionnel au nombre de tentatives d'initiations, que tous les poissons

présentent le même taux de succès d'initiation après une tentative et qu'il existe une corrélation positive entre les initiations et les vitesses moyennes de nage.

Une analyse poussée des mouvements collectifs nous fait constater que les zebrafish se déplacent essentiellement en groupe et transitent sans interruption ni périodicité entre les chambres. Nous sommes actuellement en train d'améliorer cette étude en apportant de nouveaux points de comparaison afin de vérifier si la non-périodicité des transitions entre les chambres est liée à la densité des groupes testés.

Enfin, nous nous inspirons du précédent système expérimental – les deux chambres reliées par un couloir – pour créer une version actualisée d'un labyrinthe en Y. Ce labyrinthe en Y est dit *perpétuel* car il combine tout le savoir faire que nous avons développé dans l'élaboration des précédents systèmes expérimentaux : une faible habituation des zebrafish pour leur milieu, une réduction des interactions entre l'expérimentateur et les animaux et la possibilité pour les poissons de circuler dans un labyrinthe à symétrie centrale, sans zone de départ ni zone de fin formalisées (typiques des labyrinthes en Y).

Abstract

The collective decision-making is one of the mechanisms used by social species during foraging, path optimisation, collective movements, predator avoidance or habitat selection. Zebrafish (*Danio rerio*), gregarious animal models in biology, have never been studied in the context of collective binary choices. We found logical to analyse their decision behaviours. The goal of this thesis is to meet the expectations of the ASSISI project of creation of an adjustable experimental setup able to sustain robots and fish, of development of an adaptive and self-organised mixed society and of the characterisation of individual and collective behaviours of the zebrafish, implementable in the robots.

We show that the collective decision making and the cohesion of groups of zebrafish in an open environment, composed of two identical landmarks, are dynamical processes that vary in function of the strain of *Danio rerio* (AB or TL) and are related to the density of the populations. Always on the move, the fish oscillate between the two landmarks. The AB zebrafish are more attracted by the landmarks and are less cohesive than the TL zebrafish.

In a constrained environment, two rooms connected by a corridor, we do the same type of experiments with only AB zebrafish and vary the density of the groups from 1 to 20 individuals. AB zebrafish swim together. The increase of the density of the groups make them split. We noticed that the density of the groups has an effect on the topology of the groups : during collective departures from a room to the other one, there is a correlation between the rank of exit of the zebrafish (followers) and the rank of the distances of each individual from the initiator of the exits. This correlation is higher when the followers are either the closest or the farthest from the initiator.

Using the previous experimental setup, we focused also on the topics related to leadership for groups of 2 to 10 individuals. We show that each fish initiate at least once a collective departure and that the number of initiations is proportional to the number of initiation attempts. Also, we found that all the fish have the same success rate in the initiations after an initiation attempt and that there is a positive correlation between the initiations and the average speed.

A deeper analysis of the collective movements shows that the zebrafish swim in group and transit without any interruption or even without periodicity between the rooms. We are

currently improving this study and will bring new points of comparison to check if the non-periodicity of the transitions could be related to the density of the groups.

Finally, we developed a new version of the Y-maze based on the previous observations. This *perpetual Y-maze* shows many useful features for the study of the behaviour : a low habituation rate, a reduction of the interactions between the animals and the experimentators, and allows the fish to move in a Y-maze without starting nor ending zones as in typical Y-maze.

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Chapitre 1

Introduction Générale

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Au regard de l'étendue de la recherche et des techniques actuelles, on se rend compte de l'omniprésence des comportements collectifs. On les retrouve à tous les niveaux, qu'ils soient microscopiques ou bien macroscopiques, organiques ou inorganiques.

1.1 L'individu, le social et les comportements collectifs

1.1.1 Adaptation

C'est à Darwin et son "On The Origin Of Species" (1859 – [Darwin \[1859\]](#)) que l'on doit la Théorie de l'évolution, dont le mécanisme fondamental est la sélection naturelle. Dans l'étude des comportements animal, nous nous efforçons de comprendre comment l'évolution, par la sélection naturelle, fait émerger et modifie, dans le temps, des traits comportementaux communs aux espèces.

La sélection naturelle a favorisé certaines espèces qui usent de leurs capacités collectives pour survivre. Il convient alors de faire un point sur les valeurs adaptatives de la vie en groupe et des comportements collectifs. La vie en groupe est un phénomène largement partagé dans le monde vivant puisqu'il se retrouve chez nombre d'espèces vertébrées et invertébrées. [Krause et Ruxton \[2002\]](#) ont montré qu'elle procure un avantage adaptatif face aux pressions de l'environnement.

Ainsi, en vivant en groupe, les individus augmentent leurs chances de survie face à la prédation : les prédateurs sont détectés plus facilement ([Alexander \[1974\]](#); [Chapman et Chapman \[2000\]](#); [Struhsaker \[1981\]](#); [Van Schaik et collab. \[1983\]](#)), les individus du groupe sont informés de la présence de prédateurs dans leur environnement ([Berger \[1978\]](#); [Bradbury et Vehrencamp \[1998\]](#); [Cheney et Seyfarth \[1992\]](#); [Lima \[1995\]](#); [Manser et collab. \[2002\]](#); [Zuberbühler \[2001\]](#), *collective vigilance*) et peuvent par la suite se coordonner pour se défendre ([Abrol \[2006\]](#); [Chapman et Chapman \[2000\]](#); [Côté et Gross \[1993\]](#); [Kenward \[1978\]](#); [Seeley et collab. \[1982\]](#), *group defense, predator confusion and encounter dilution effect*). De même, vivre en groupe, confère un avantage dans la recherche de nourriture : l'exploration de l'environnement est plus efficace et les individus découvrant une source de nourriture partagent l'information au groupe ([Caraco \[1979\]](#); [Janson et Di Bitetti \[1997\]](#); [Schmitt et Strand \[1982\]](#); [Street et Hart \[1985\]](#)).

1.1.2 De l'individu au groupe

Interaction et transfert d'informations

[Sumpter \[2010\]](#) résume très bien la nécessité de vivre en groupe : "A key benefit of being near to others is access to information". Les mécanismes utilisés pour transférer l'information sont très variés. [Cosnier \[1977\]](#) montre ainsi que la communication com-

prend "des signaux de diverse nature : sonores, gestuels, mimiques, posturaux, chimiques, thermiques, tactiles, voire électriques". Néanmoins, selon les taxons monophylétiques (ou clades), il semble persister une certaine similitude des mécanismes de communication. On serait même tenté de les classer : le signalement actif où les espèces usent de phéromones, s'échangent de la nourriture (*trophallaxie*), effectuent des mouvements spécifiques ou les divers signaux cités par Cosnier, le signalement par indices, à savoir les déplacements collectifs et autres bancs plus ou moins structurés.

La première source d'information, quand des individus reviennent avec une ressource dans le nid, est la ressource elle-même. Sa qualité tout comme des indices de sa provenance peuvent être identifiés grâce à son odeur et à la direction du vent. Par la suite, les congénères qui n'étaient pas présents lors de la trouvaille vont utiliser les informations données par les colporteurs. Ce transfert d'information, qui a lieu dans le nid et ne concerne que la localisation de la ressource, peut être d'ordre chimique, comme chez les fourmis qui déposent des phéromones du nid jusqu'à la ressource, ou visuel, comme chez les abeilles qui dansent pour indiquer la direction de la zone à visiter. Parfois l'information donnée par un des membres n'indique plus une position mais suggère le type de ressource dont la colonie a besoin. C'est le cas des chauve-souris *Carollia perspicillata* qui utilisent leurs perchoirs comme des centres d'échange d'informations quant à la présence de ressources éphémères intéressantes pour le groupe (Ratcliffe et ter Hofstede [2005]). Juchées au-dessus du sol, ces chauve-souris échangent des indices chimiques de présence de nourriture apte à la consommation.

Pour les animaux n'ayant pas de centre d'échange d'informations, les individus non-informés copient les réactions de ceux qui ont l'information. En 1973, Radakov [1973] a montré que la propagation d'informations directionnelles est plus rapide que le déplacement des individus. Ici, en modifiant leur direction chaque poisson stimulait ses propres voisins/copieurs. Drent et Swierstra [1977] ont construit des leurres d'oies à tête baissée ou à tête relevée et les ont regroupés en fonction de ce paramètre. La tête baissée est censée marquer la présence de nourriture au sol. Ils ont remarqué que les volées d'oies atterrissent préférentiellement près des groupes de leurres d'oies à tête baissée, et suggèrent que les oies testées copient le comportement des leurres mimant la présence de nourriture. Dans certains cas, la copie donne naissance à un autre phénomène : le mécanisme en quorum. Quand le quorum (un nombre particulier d'individus) est atteint, la probabilité de mener une action explose.

D'ailleurs, il arrive souvent que la communication passe par de multiples canaux. C'est le cas chez les primates (comme le *Cercopithecus talapoin*) où Gautier et Gautier-Hion [1977] mettent en avant une association de la vocalisation à certaines mimiques faciales. Enfin, nous ne pouvons pas cantonner le transfert d'information qu'aux essentiels processus de défense et de récolte de nourriture. La communication est aussi utilisée

par les individus dans le but de perpétuer l'espèce (appel du mâle, parade nuptiale, etc.) voire même de transmettre le savoir (Fisher et Hinde [1949]) et la culture (Whiten et collab. [1999]).

Nous verrons dans la sous-partie intitulée *Auto-organisation* d'autres mécanismes de relais d'informations.

Les degrés de la socialité

Camazine [2003] définit spatialement l'agrégation comme tout assemblage d'individus de densité supérieure aux régions avoisinantes. Ce phénomène est polyphylétique, puisqu'on le retrouve chez certaines bactéries et dans différents groupes zoologiques. Les agrégats peuvent être issus de facteurs non sociaux : des pressions environnementales, comme l'hétérogénéité d'un milieu, peuvent regrouper des individus sans qu'ils aient la moindre incidence sur leur déplacement (agrégation passive); des individus se déplacent vers une source d'attraction (agrégation active). Parallèlement, des facteurs sociaux peuvent aussi influencer sur l'agrégation, on parle alors d'interattraction (attraction mutuelle).

La socialité est la tendance d'une population animale à vivre en groupe. C'est l'interattraction entre des individus qui forge la vie sociale. On distingue divers degrés de socialité dans le monde vivant, définis selon le niveau de complexité des comportements sociaux des individus d'un groupe.

Lorsque des individus de la même espèce se regroupent, sans relation préférentielles, c'est à dire ni sexuelles, ni parentales, ni environnementales, on parle de *grégarisme*. Les groupes formés sont temporaires et confèrent à leurs membres un avantage face aux pressions de l'environnement. Cette forme de vie sociale est répandue puisqu'elle se retrouve chez les blattes (Bell et collab. [2007]), chez les poissons formant des bancs (Hoare et collab. [2000]; Krause et Ruxton [2002]; Parrish et Hamner [1997]; Reebs [2000]) ou les animaux volant en nuées (Ballerini et collab. [2008b]; Powell [1974]).

Le stade *subsocial* est défini par l'apparition des comportements parentaux, soit l'investissement énergétique des parents dans chaque descendant afin d'accroître ses chances de survie (Robert [1972]). On retrouve ce stade social chez les coléoptères bousiers du genre *Copris* (Halffter [1997]), certains amphibiens, comme le crapaud accoucheur, *Alytes obstetricans*, le crapaud *Rhinoderma* et aussi chez tous les mammifères et oiseaux (Aron et Passera [2009]).

Quand le soin aux jeunes se réalise dans un site d'élevage commun à plusieurs femelles, on qualifie l'espèce de *coloniale*. Il n'y a pas de coopération entre les femelles lors des soins prodigués aux jeunes. De nombreuses sociétés de coléoptères Scolytidae sont dites coloniales. Les femelles pondent leurs oeufs dans des réseaux de galeries creusés dans le bois; les larves s'y développeront par la suite.

C'est la coopération dans le soin aux jeunes qui définit les espèce *communales*. Par exemple, les nécrophores transportent à plusieurs les cadavres d'animaux et les femelles, sans distinction, nourrissent les jeunes larves dans la loge centrale de la niche (Aron et Passera [2009]).

Le mode de vie sociale le plus complexe est le stade *eusocial*, il y coopération dans les soins apportés aux jeunes entre des individus spécialisés dans la reproduction et issus au minimum de deux générations (Wilson [2000]). Avec une telle définition, il ne concerne essentiellement que les fourmis, les termites et certaines espèces d'abeilles et de guêpes. Seulement deux espèces mammifères appliquent ce mode de vie sociale : le rat taupe nu (*Heterocephalus glaber*) et le rat taupe de Damar (*Cryptomys damarensis*), espèces vivant en groupe d'individus spécialisés où une seule femelle se reproduit, les autres étant socialement castrées (Jarvis et collab. [1994]).

Nous rappelons les différents niveaux de socialité dans le Tableau 1.1.

Degrés de socialité	Interattraction	Comportements parentaux	Site d'élevage commun	Coopération dans les soins aux jeunes	Spécialisation dans la reproduction
Solitaire					
Grégaire	+				
Subsocial	+	+			
Colonial	+	+	+		
Communal	+	+	+	+	
Eusocial	+	+	+	+	+

TABEAU 1.1 – Les degrés de la socialité selon Aron et Passera [2009].

La cohésion du groupe

En réponse aux pressions de son environnement, le groupe voit sa densité et sa forme fluctuer, aussi bien au niveau local que dans sa globalité (Cavagna et collab. [2010]). Pour maintenir sa cohésion, chaque membre du groupe utilise des informations locales délivrées par ses sens. Ainsi, Ballerini et collab. [2008a] ont montré que la cohésion d'une volée d'étourneaux (*Sturnus vulgaris*) de plusieurs milliers d'individus s'appuie essentiellement sur les quelques interactions locales entre animaux : chaque oiseau n'interagit qu'avec les six ou sept congénères les plus proches. Cette découverte a eu un impact majeur dans les développements de modèles de bancs d'animaux.

Parfois, le groupe est mené à se séparer et se reformer, on parle alors de mécanisme de fission-fusion. Il est commun dans le monde vivant et génère nombre d'avantages (Silk et collab. [2014]). Par exemple, chez la chauve souris Vespertilion de Bechstein (*Myotis*

bechsteinii), il participe au transfert d'informations entre les sous-groupes et le groupe [Sueur et collab. \[2011\]](#), chez les poissons *Fundulus diaphanus*, *Notemigonus crysoleucas*, *Catostomus commersonii*, *Poecilia reticulata*, il peut être à l'origine de regroupements par taille de corps ([Croft et collab. \[2003\]](#); [Hoare et collab. \[2000\]](#); [Krause et Ruxton \[2002\]](#)).

Il convient alors de définir quelques termes relatifs à la cohésion :

shoal : regroupement de poissons pour des raisons sociales.

school : regroupement de poissons se déplaçant de façon coordonnée dans la même direction.

flock : regroupement d'oiseaux en déplacement ou en approvisionnement.

swarm : agrégat d'animaux de tailles similaires se déplaçant en masse.

L'individualité dans un groupe

Le groupe agissant de façon coordonnée on aurait tendance à imaginer que tous ses membres sont à la fois identiques et interchangeable. Néanmoins, la réalité montre qu'ils sont tous différents et présentent des variations génétiques, phénotypiques, sexuelles voire même comportementales. Cette diversité, n'est pas sans conséquence sur les décisions collectives. Les abeilles présentent dès leur plus jeune âge des niveaux variables de réponses au sucrose ce qui déterminera par la suite leur inclination à récolter plutôt de l'eau, du nectar ou du pollen ([Pankiw et Page Jr \[2000\]](#)). Ainsi, en favorisant la diversité, les abeilles s'adaptent plus facilement aux pénuries : si une ressource viendrait à manquer, le reste de la colonie est déjà en charge d'en approvisionner une autre. On verra, dans la partie sur l'auto-organisation, que certaines épinoches plus téméraires que d'autres, explorent leur environnement plus volontiers et initient plus souvent des déplacements collectifs ([Harcourt et collab. \[2009\]](#)). [Bret \[2014\]](#) a fait sa thèse sur le thème de l'individualité et son rôle dans la cohésion des groupes de primates. Elle remarque que la personnalité est bien liée au statut social et que seulement certains individus permettent la cohésion entre les groupes et à l'intérieur de ces groupes.

1.1.3 Souches et comportements

D'année en année, la recherche sur les comportements animal s'affine. Alors que nous pensions avoir compris les interactions entre individus et après avoir décrit des règles générales sur les comportements des espèces étudiées, nous devons garder à l'esprit que tout peut être remis en question. Ainsi, avec l'essor des connaissances en biologie et la possibilité d'étudier de façon plus pointilleuse les comportements de certaines espèces, il ressort que l'observation des souches d'une même espèce fait émerger des grandes variabilités comportementales. Dans un domaine assez proche de celui des comportements collectifs, à savoir les comportements individuels, [de Esch et collab. \[2012\]](#); [Lange et col-](#)

lab. [2013], qui travaillent sur des larves de poissons zèbres (ou zebrafish), *Danio rerio*, ont montré que selon la souche (AB, TL, ABstrg, casper, EK, TU et WIK) les larves nagent ou plus longtemps ou plus rapidement ou sur une plus longue distance. De même, chez les mammifères, [Rex et collab. \[1996\]](#) ont remarqué que des rats de différentes souches (Wistar, Lewis, Fischer, Brown et Norway) présentent des comportements différents face à la peur, y compris chez des souris [Griebel et collab. \[2000\]](#) (avec les souches BALB/c, C57BL/6, C3H, CBA, DBA/2, NMRI, NZB, SJL et Swiss). Dans le domaine des comportements collectifs, les scientifiques ont écrit de grandes généralités en s'appuyant sur les modèles qu'ils ont développé à partir de données expérimentales. Loin de vouloir remettre en question ces avancées – la généralisation a toujours été utile pour comprendre et expliquer des phénomènes bien plus complexes –, j'ai gardé à l'esprit les faits cités ci-dessus et développé, dans les débuts de ma thèse, une recherche prospective sur les comportements collectifs des souches de zebrafish. C'est d'ailleurs un point développé dans le manuscrit.

1.2 Gestion du groupe et prise de décision

Il existe une multitude de situations durant lesquelles les animaux sont confrontés à des choix imposés par leur environnement. La recherche de nourriture ([Janson et Di Bitetti \[1997\]](#)), la détection de prédateurs ([Berger \[1978\]](#); [Bradbury et Vehrencamp \[1998\]](#); [Cheney et Seyfarth \[1992\]](#); [Lima \[1995\]](#); [Manser et collab. \[2002\]](#); [Zuberbühler \[2001\]](#)), la sélection d'un habitat ou d'un territoire ([Franks et collab. \[2002\]](#); [Séguret et collab. \[2016\]](#)) sont autant d'événements impliquant des prises de décisions. Le choix se définit comme une sélection entre deux ou plusieurs alternatives qui aura un impact direct sur la survie de l'animal.

Chez les animaux sociaux, les notions de groupe et de transfert d'information sont primordiales lors de ces événements et il devient rapidement nécessaire de faire le point sur les alternatives proposées. On parle alors de prise de décision collective. Faisant partie d'un tout, les individualités s'effacent en partie ou totalement et les décisions de chaque individu sont influencées à plus ou moins grande échelle par les comportements des congénères.

1.2.1 Auto-organisation

Principe

L'auto-organisation est un phénomène de mise en ordre d'éléments indépendants et autonomes. Dans *Self-organization in Nonequilibrium Systems* ([Nicolis et collab. \[1977\]](#)), les auteurs remarquent l'existence d'autant de "preuves expérimentales que d'observa-

tions, montrant des systèmes impliquant un grand nombre de sous-unités en interactions pouvant présenter, sous certaines conditions, une cohérence comportementale dépassant la cadre de la sous-unité individuelle". En avançant l'idée d'une "cohérence comportementale dépassant la cadre de la sous-unité individuelle", les auteurs définissent alors l'auto-organisation comme indépendante de toute procédure, de tout plan pré-établi d'organisation ou de détails individuels. Ainsi, l'assertion "La totalité est plus que la somme des parties" (Aristote) est directement lié aux systèmes auto-organisés et le champ de recherche qui en découle. Depuis, l'auto-organisation a permis de décrire de nombreux phénomènes dans les systèmes physiques (supraconductivité, cristallisation, convection, etc.), chimiques (auto-assemblage moléculaire, micelles, cristal liquide, etc.) ou biologiques. Dans les systèmes biologiques, c'est elle qui fait émerger des structures aussi complexes que des vagues en spirales de chimioattractants dans des colonies de *Dictyostelium discoideum* (Ball [2009]), la forme hexagonale des alvéoles d'abeilles (Ball [2009]; Karihaloo et collab. [2013]), les diverses formes et tailles des bancs de poissons (Parrish et collab. [2002]; Partridge [1982]; Partridge et collab. [1983]) ou la synchronisation des applaudissements (Néda et collab. [2000a,b]).

Mécanismes

Une de ces propriétés est la boucle de rétroaction positive. Une boucle de rétroaction est un cycle de processus agissant en chaîne. La boucle de rétroaction positive prend forme lorsque toutes les rétroactions entre les différents chaînons conduisent à amplifier un signal, une perturbation ou une action (Sumpter et Pratt [2009]). Ce mécanisme est très commun dans le vivant : operon lac chez *E. coli*, hypercytokinémie, génération d'influx nerveux, ... Dans les groupes ou sociétés d'animaux, c'est lui qui construit les motifs collectifs. Ainsi, Ame et collab. [2004] ont montré qu'en présence d'un choix binaire (deux abris identiques), le consensus est atteint par les cafards *Blattella germanica* qui sélectionnent alors majoritairement (à 80%) un des deux abris : un premier cafard s'abrite, puis un deuxième à côté, etc. Lors des migrations de fourmis *Temnothorax al-bipennis* et d'abeilles *Apis mellifera* vers leur nouveau nid, les stratégies mises en places sont relativement similaires (Franks et collab. [2002]). Le recrutement par les premières exploratrices de nouvelles exploratrices est dépendant de l'évaluation qu'elles font individuellement du potentiel futur nid. Ces dernières exploratrices en recrutent alors de nouvelles, ce qui génère une boucle de rétroaction positive (Mallon et collab. [2001]; Seeley et Visscher [2004a]; Seeley et Buhrman [1999]). Le potentiel nid est progressivement rempli de visiteuses. Chez les fourmis, dès que le seuil de population du potentiel nid est atteint (quorum), ce dernier le devient pleinement ce qui amorce alors le déménagement de la reine et des larves (Pratt et collab. [2002, 2005]). Chez les abeilles, le quorum dépassé, les exploratrices retrouvent leurs congénères dans l'ancien nid et déclenchent le compor-

tement dit de "piping" (Seeley et Visscher [2003, 2004b]) qui prépare la sortie du nid. Elles guideront ensuite l'essaim vers le nouveau nid. Il est très rare que le quorum soit atteint pour plusieurs nids potentiels. Chez les poissons *Gasterosteus aculeatus*, il a été démontré l'existence de boucle de rétroaction positive lors de prises de décisions collectives. En effet, Ward et collab. [2008] ont proposé un choix binaire de couloirs avec un et/ou deux réplicat(s) de l'espèce se déplaçant chacun vers l'un et l'autre couloir, à plusieurs tailles de populations de poissons. Ils ont montré que les individus (1) choisissent préférentiellement l'option sélectionnée par la majorité quand un seul des réplicats est utilisé, (2) se partagent en deux groupes égaux lorsque les deux réplicats sont utilisés, ce qui se caractérise par une distribution en U de la proportion des poissons qui décident d'aller d'un côté ou de l'autre. Cette distribution est caractéristique d'une boucle de rétroaction positive.

La boucle de rétroaction négative propose l'effet inverse de la boucle de rétroaction positive et inhibe l'action. Dans les groupes ou sociétés d'animaux, elle participe de la stabilisation des motifs collectifs émergents (Camazine [2003]). Elle peut être issue de causes externes, tel l'épuisement des ressources en nourriture, ou internes à la population, comme le nombre limité de glaneurs. Elle peut être aussi déclenchée par des signaux spécifiques lors d'attaques de prédateurs près des sources de nourriture, ce qui fera décroître le recrutement des individus (Nieh [2010]; Robinson et collab. [2005]).

Bien sûr, ces deux boucles sont dépendantes, comme on a pu le voir, de stimuli qui, s'ils dépassent une valeur seuil, déclenchent le processus. C'est le seuil de réponse (à un manque ou un trop plein de nourriture, la présence de prédateurs, épidémie, etc.). Il n'existe pas de valeur universelle de seuil et c'est bien au cas par cas qu'on l'identifie (Sumpter [2006]).

1.2.2 Leadership

La question du leadership est un point attracteur en sciences sociales. Elle est souvent mise en relation avec des concepts politiques, commerciaux, moraux, ... On définit alors le leadership comme "[l']autorité exercée par une personne ou groupe de personnes sur un groupe qu'elle ou il représente" (wiktionnaire). En biologie, elle est concomitante des recherches sur les comportements collectifs, à savoir les déplacements, l'approvisionnement, l'apprentissage, etc. Qui bouge? À quel instant? Pour aller où? Pour quoi faire? Avec quelle organisation? sont autant de questions qui s'y rapportent. L'idée que nous nous faisons du leadership est beaucoup plus quantifiable, puisqu'il est visible lors d'actions bien précises. Il se définit alors comme l'initiation de nouveaux déplacements ou comportements d'un ou plusieurs individus suivis par les autres membres du groupe (Dyer et collab. [2009]; Krause et collab. [2000]). Néanmoins, King [2010] remet en question cette

définition dès lors qu'elle ne traite que des succès d'initiation. [Petit et Bon \[2010\]](#) résolvent le problème et proposent un terme supplémentaire : *initiateur*, ce qui implique d'ailleurs l'existence de *suiveurs*. L'intérêt ici étant de combiner la notion de réussite ou d'échec à l'initiation et de se demander si un initiateur qui a échoué peut devenir initiateur qui réussit et inversement. L'idée étant toujours d'affiner la notion de leadership.

On parle de *leadership personnel* lorsqu'un individu initie seul les activités du groupe. Cette capacité est inhérente aux groupes ou sociétés hiérarchisés. Le statut de dominant peut être dévolu à l'individu le plus vieux qui endosse alors, à lui seul, la responsabilité de la reproduction et de la protection de son harem, c'est le cas les gorilles des montagnes (*Gorilla beringei beringei*) selon [Aron et Passera \[2009\]](#); [Watts \[2000\]](#). Chez les loups (*Canis lupus*) ([Mech \[2012\]](#)) et les mangoustes naines du Sud (*Helogale parvula*) ([Anne et Rasa \[1983\]](#)), c'est un couple dominant qui assure le leadership. Étant plus autonome, le dominant augmente ses chances d'être le premier à agir, d'autant plus qu'il exerce sur le groupe une influence très forte ([Krause et collab. \[2009\]](#)). Ce pacte social ne fonctionne que si tous les membres du groupe reconnaissent un seul individu ou couple comme leader. Si leurs intérêts divergent de ceux du dominant, c'est toute la hiérarchie sociale qui est touchée. Le leader doit réaffirmer sa position ou cède sa place à un nouveau leader. On retrouve quelque peu ce système de leadership chez d'autres animaux où la gestion du groupe est, cette fois-ci, établie par plusieurs individus présents en haut de la hiérarchie, par exemple, chez les macaques rhésus (*Macaca mulatta*) ([Sueur et Petit \[2008\]](#)) et les dauphins (*Tursiops sp.*) ([Lusseau \[2007\]](#)).

À contrario, lorsque le leadership n'est pas attribué à un individu en particulier, on dit de lui qu'il est *distribué*. Tous les membres du groupe peuvent initier une activité collective quelque soit leur position dans la hiérarchie. À ce moment, d'autres facteurs rentrent en jeu, tels que la motivation, la position par rapport au groupe, les capacités personnelles, la personnalité et même la détention d'informations vitales. [Collignon et collab. \[2012\]](#); [Collignon et Detrain \[2009\]](#) remarquent que le leadership distribué, parmi quelques individus de la colonie, est extrêmement profitable au recrutement de nouvelles fourmis (*Tetramorium caespitum*) lors des activités d'approvisionnement. Aussi, chez le zèbre (*Equus burchellii*) ([Fischhoff et collab. \[2007\]](#)), le bar commun (*Dicentrarchus labrax*) ([Millot et collab. \[2009\]](#)) ou l'épinoche (*Gasterosteus aculeatus*) ([Nakayama et collab. \[2012\]](#)), les individus momentanément plus motivés initient les déplacements collectifs. Chez le sapajou capucin (*Cebus capucinus*) ([Leca et collab. \[2003\]](#)) et le macaque rhésus (*Macaca mulatta*) ([Sueur et Petit \[2008\]](#)), les individus au centre du groupe initient des déplacements collectifs alors que chez le méné jaune (*Notemigonus crysoleucas*) ([Reebs \[2000\]](#); [Rosenthal et collab. \[2015\]](#)), le gardon (*Rutilus rutilus*) et l'épinoche ([Bumann et Krause \[1993\]](#); [Krause et collab. \[2000\]](#)), ce sont les individus en périphérie du groupe. [Petit et collab. \[2015\]](#) remarquent que chez les pigeons (*Columba livia*), très hiérarchisés, les

plus rapides d'entre eux (capacités personnelles) sont très souvent des leaders. [Harcourt et collab. \[2009\]](#) ont remarqué que certaines épinoches sont plus téméraires que d'autres, explorent leur environnement plus volontiers et initient plus souvent des déplacements collectifs en recrutant facilement les individus peureux.

Dans certains cas, le leadership est encore plus partagé. [Sueur et Petit \[2008\]](#) ont remarqué que les macaques de Tonkean (*Macaca tonkeana*) sont égalitaires dans la gestion des déplacements du groupe.

1.2.3 Consensus

Types de consensus

Une décision de consensus est atteinte lorsque tout un groupe choisit une alternative parmi plusieurs, exclusives ([Conradt et Roper \[2005\]](#)). Lors du processus de décision, tous les membres du groupe décident individuellement en fonction des informations locales, et afin de satisfaire leurs besoins. Au gré des tendances et des transferts d'informations, la décision atteint un équilibre. Dans leur article, [Conradt et Roper](#) poussent leur analyse du consensus jusqu'à proposer les termes *consensus partagé*, *consensus non-partagé* et *consensus partiellement partagé*.

Le *consensus partagé* a déjà été développé ci-dessus. On le retrouve notamment chez les vertébrés non-humains, comme les diamants mandarins, (*Taeniopygia guttata*), les oies à tête barrée (*Anser indicus*) ou encore les sapajous capucins (*Cebus capucinus*) ([Conradt et List \[2009\]](#); [Conradt et Roper \[2005\]](#)). Il peut engendrer de profonds conflits d'intérêts et être assimilé au leadership distribué.

Le *consensus non-partagé* survient lorsqu'un individu prend une décision pour la communauté, qui s'y soumet; il peut être assimilé au leadership personnel.

Le *consensus partiellement partagé* est déclaré quand une proportion de la population contribue à la prise de décision. Il n'y a pas de leader dans la population, juste des individus qui possèdent plus d'informations que les autres au début du processus de prise de décision, qu'ils initieront ([Jeanson et collab. \[2014\]](#)). [Seeley \[2003\]](#); [Seeley et Buhrman \[1999\]](#) prennent pour exemple les abeilles *Apis mellifera*, où seulement 5% des ouvrières qui explorent l'environnement autour de la ruche participent aux prises de décision concernant leur nouveau nid. [Couzin et collab. \[2005\]](#) proposent un modèle de *consensus partiellement partagé* : des individus informés ne sachant ni leur identité, ni leur nombre entraînent d'autres individus non-informés vers une source de nourriture. On observe alors qu'ils réussissent leur action avec précision bien qu'en proportions faibles. Il existe enfin certains cas particuliers où plus le groupe est grand, plus la prise de décision est partagée : les pigeons (*Columba livia*) et les alouettes des champs (*Alauda arvensis*), usent de ce processus ([Conradt et Roper \[2005\]](#)). On constate peu ou plus de

conflits d'intérêts.

Quoi qu'il en soit, le consensus n'existe, que si tous les individus, participant ou non à la décision, la respectent. Chez le méné jaune (*Notemigonus crysoleucas*), l'orientation imposée au groupe par des individus informés est remise en question dès lors que l'égalité entre les nombres d'individus informés et non informés est atteinte (Couzin et collab. [2011]). Mécanisme préservant la cohésion, renforçant la précision de la décision par rapport à un individu seul et améliorant la vitesse de décision, il doit donc satisfaire les intérêts de tous les membres du groupe. Enfin, cette description exclusive des différents types de consensus ne reflète pas la réalité. La frontière entre chaque type de consensus est bien plus perméable qu'on ne le pense : chez le loup, la mangouste ou le gorille des montagnes où les dominants semblent être à l'origine des déplacements collectifs, il a été remarqué une activité de pré-départ de l'ensemble du groupe qui indique aux dominants que la meute est prête à partir (Holekamp et collab. [2000]; Stewart et Harcourt [1994]). Ici, les dominants prennent la décision de déplacer le groupe à la suite d'une démarche de *consensus partagé*.

***Many-wrongs* principe et précision**

Application du théorème central limite qui prédit que l'erreur à la moyenne est inversement proportionnelle à la racine carrée de la taille d'une population, le *many-wrongs* principe (la sagesse des foules) montre que la moyenne des choix indépendants (intégrant toute la variabilité des choix) effectués par une population d'individus non biaisés tend avec précision vers la réalité observée et contraste avec le choix d'un seul individu pris au hasard (Simons [2004]; Wallraff [1978]). Les observations de Galton [1907] ont montré l'existence du phénomène. En proposant à 800 personnes de deviner le poids d'un bovin et en moyennant les résultats des estimations, il trouve que la différence entre le poids effectif du bovin (544.5 kg) et la médiane des estimations est de 450g. Ce principe a maintes fois été vérifié chez d'autres espèces. La moyenne de la direction des danses des abeilles *Apis florea* dans leur ruche orientant vers de nouveaux nids est similaire à la direction que l'essaim choisira (Oldroyd et collab. [2008]). Chez les alouettes des champs et les pigeons, c'est encore une fois le vol en nuée qui améliore les capacités d'orientation et de navigation des oiseaux, selon Perera et Guilford [1999]; Rabøl et Noer [1973].

1.3 Déplacements collectifs

On a vu dans la partie précédente que les déplacements collectifs sont intimement liés à la prise de décision et que l'auto-organisation et les différentes formes de consensus et de leaderships, exclusivement ou non, participent à l'essentiel de celle-ci. Les déplacements collectifs peuvent se diviser en trois phases : le pré-départ, l'initiation et la pro-

gression. Pour des événements de déplacements collectifs, [Krause et collab. \[2000\]](#) ont apporté une définition claire du leadership, et surtout objective, que nous utiliserons désormais : c'est l'initiation de nouvelles directions de locomotions suivies par les autres membres du groupe.

1.3.1 Pré-départ

La période de pré-départ est un moment étalé dans le temps, de l'ordre de quelques minutes, durant lequel les membres du groupe échangent des informations quant à une future action, se jaugent, se feignent. Dans certains cas, elle est marquée par l'action d'une partie du groupe. [Bourjade et collab. \[2015, 2009\]](#) remarquent une activité accrue chez les chevaux *Equus ferus przewalskii* avec des comportements bien spécifiques : certains s'éloignent du groupe, d'autres les suivent, d'autres encore se placent en périphérie tout en étant rejoints par des congénères. [Ramseyer et collab. \[2009a\]](#) mettent en avant, deux minutes avant un départ collectif d'oies domestiques (*Anser anser domesticus*) au repos, de profonds changements de vigilance, l'amplification d'échanges sonores ou des ailes qui battent. Chez les bovins, [Ramseyer et collab. \[2009b\]](#) montrent que la période de pré-départ se caractérise par des augmentations de la vigilance et des mouvements de tête et la prégnance du silence. Dans d'autres cas, il arrive qu'elle soit liée à une prise de décision collective de type consensus. C'est ce que [Ward et collab. \[2008\]](#) ont montré chez *Gasterosteus aculeatus*, [Conradt et List \[2009\]](#); [Conradt et Roper \[2005\]](#) chez *Taeniopygia guttata*, *Anser indicus* ou encore *Cebus capucinus* et [Seeley \[2003\]](#); [Seeley et Buhrman \[1999\]](#) chez *Apis mellifera* (cités plus haut). Bien que maintes fois observée et quantifiée cette période de pré-départ n'est pas universelle. On ne peut pas dire si tous les animaux sociaux étudiés, à l'heure actuelle, adoptent des comportements de pré-départ. Ceci à cause des moyens et des méthodes d'analyse. Il est possible que, dans un futur proche, l'on ait développé de nouveaux outils qui quantifieront précisément ces comportements.

1.3.2 Initiation

L'initiation précède le départ collectif, elle en est une tentative fructueuse. Elle se situe dans l'instant. Le groupe sait seulement qu'il va partir. Si l'initiation échoue, le départ collectif n'a pas lieu. Le-s initiateur-s doit/doivent alors maximiser ses/leurs chances de convaincre les autres de le-s suivre (c'est à dire se faire connaître de tous), et le groupe doit réagir aux stimuli envoyés par tous les membres (trouver le-s initiateur-s). Dans les groupes hiérarchisés où l'initiateur est déjà connu de tous, reconnaître l'initiation paraît plus simple puisqu'il suffit d'attendre la réaction du/des leader-s. Néanmoins, on a vu que le leader initiait un départ collectif s'il savait que tous les membres de son groupe étaient prêts. Dans des populations moins hiérarchisés, [Pillot et collab. \[2010\]](#) montrent

qu'un mouton (*Ovis aries*) qui s'éloigne du groupe peut lancer un départ collectif, tout comme chez l'épinoche (Leblond et Reeb [2006]). Leca et collab. [2003]; Petit et collab. [2009] remarquent encore que les sapajous capucins doivent synchroniser leurs comportements avec une fraction minimale de congénères pour lancer un départ collectif. Ici, la tâche des chercheurs est plus ardue : il s'agit de différencier une réponse à un stimulus extérieur, d'une synchronisation des comportements résultant d'interactions sociales. C'est ce qu'ont développé Pillot et collab. [2011] chez le mouton.

Si l'initiation est un échec, il n'y a pas de départ collectif. En étudiant les départs collectifs de sapajous capucins, Petit et collab. [2009] ont remarqué, entre autre, l'inclination de l'initiateur peu suivi à abandonner son action. En-dessous d'une certaine proportion d'individus suivant l'initiateur, ce dernier renonce et retourne se reposer.

1.3.3 Progression

Si l'initiation est couronnée de succès, le départ collectif est alors déclenché. Les individus doivent coopérer afin de réduire les risques de prédation (Altmann [1979]; Hockings et collab. [2006]; Rhine et Tilson [1987]) ou d'atteindre leur objectif sans égarer un membre distrait. En fonction des caractères intrinsèques des membres, la progression peut s'effectuer en groupes plus ou moins soudés (Croft et collab. [2003]; Hoare et collab. [2000]; Krause et Ruxton [2002]), selon les affinités (Briard et collab. [2015]) ou les tempéraments (Harcourt et collab. [2009]). En se déplaçant ainsi, ils ne sont plus de simples proies statiques et procèdent non seulement à la reconnaissance de leur environnement mais aussi à la détection des ressources en nourritures.

Herbert-Read [2016] a passé en revue l'organisation des groupes d'animaux en déplacement. Il en ressort une grande disparité. Se déplaçant sur un plan horizontal, les larves de criquets australiens (*Chortoicetes terminifera*) s'organisent de façon isotropique, c'est à dire que la distribution des voisins les plus proches de la larve ciblée est uniforme dans toutes les directions (Buhl et collab. [2012]). En comparaison, chez l'oiseau Macreuse à front blanc (*Melanitta perspicillata*), nageant à la surface de l'eau, ou bien des couples de poissons comme le mosquitofish (*Gambusia holbrooki*), le méné jaune et le vairon (*Phoxinus phoxinus*), les voisins les plus proches de l'individu cible se positionnent le plus souvent devant ou derrière lui (anisotropique) (Herbert-Read et collab. [2011]; Katz et collab. [2011]; Lukeman et collab. [2010]). Chez d'autres espèces, encore, les poissons danios géants (*Danio aequipinnatus*) ou les pigeons bisets (*Columba livia*) et les étourneaux sansonnets (*Sturnus vulgaris*), on retrouve les voisins de part et d'autre de l'individu cible (Ballerini et collab. [2008a]; Grünbaum et collab. [2005]; Pettit et collab. [2013]), voire même dans sa diagonale, guppies femelles (*Poecilia reticulata*). Bien entendu, en rajoutant un degré de liberté (du plan à l'espace), on augmente encore la variabilité de

l'organisation spatiale (Ballerini et collab. [2008a]; Partridge et collab. [1980]). On verra dans la suite de la thèse que l'organisation spatiale de groupes d'animaux, en l'occurrence *Danio rerio*, peut même être dépendante d'autres facteurs propres aux souches.

Dans certains cas, les groupes transitent entre différentes zones d'intérêts. C'est ce que je montrerai, d'ailleurs, dans cette thèse (Séguret et collab. [2016]). Ces oscillations peuvent être à l'origine de différences comportementales individuelles parmi les membres du groupe. Dahlbom et collab. [2011]; Guayasamin [2013] mettent en évidence des caractères individuels chez les zebrafish qui influent sur leur capacité à explorer de nouveaux environnements. Ainsi, les plus téméraires s'aventurent plus facilement dans l'inconnu. Harcourt et collab. [2009] vont plus loin dans cette analyse en étudiant l'influence des épinoches téméraires sur les épinoches peureuses, et inversement. Les poissons sont placés dans un système expérimental en couloir, partagé dans la longueur par une plaque transparente. Le couloir présente deux zones distinctes : une zone avec des feuillages l'autre avec de la nourriture. Comme on l'attend, le poisson téméraire sort plus aisément et le peureux présente une probabilité de le suivre aussi forte que de faire demi-tour. Par contre, si le poisson peureux sort le premier, le téméraire le rejoint et reste avec lui.

Comme on peut le comprendre, il existe un lien très fort entre les oscillations et les départs collectifs puisque les uns ne sont qu'une reproduction en boucle des autres. Néanmoins, toutes ces expériences de transitions/oscillations, réalisées jusqu'alors, ne prennent en compte que l'intérêt instantané des animaux étudiés et n'établissent pas de comparatifs sur le long terme. On pourrait s'attendre soit à une modification comportementale des suiveurs qui tendrait vers les tempéraments des initiateurs, soit une moyenne entre tempéraments, avec les uns qui se surpasseraient, les autres se réfréinant, ou bien l'émergence d'un comportement relatif au groupe. C'est d'ailleurs, ce que Herbert-Read et collab. [2013] expliquent chez le mosquitofish : plus la taille du groupe augmente, plus les comportements individuels s'effacent. Ils appellent cela la conformité.

1.3.4 Modélisation

Les modèles sont là pour aiguiller le-a chercheur-se et synthétiser une idée. Il existe une grande quantité de modèles, plus ou moins complexes, qui permettent à la fois de comprendre les mécanismes collectifs, de les prévoir et même de les reproduire sous forme de simulations. Il faut garder à l'esprit que plus un modèle est complexe, plus il a tendance à tendre vers la réalité observée tout en devenant moins compréhensible et anticipable. Enfin, un bon modèle s'appuie sur des variables et des paramètres mesurés expérimentalement. Selon que l'on s'intéresse à la population ou aux individus formant la population, on choisira un modèle macroscopique ou microscopique. Le modèle macroscopique essaye de définir l'état instantané d'un système (population) en utilisant un

certain nombre de variables (moyenne, concentration, quantité, etc.) [Camazine \[2003\]](#); [Sumpter \[2010\]](#). Le modèle microscopique (Agent-based modeling) fait intervenir des entités autonomes (individus) auxquelles on a imposé un ensemble de variables (position, vitesse, etc.) et dont l'état instantané des agents dépend uniquement des états précédents.

Prise de décision

On retrouve, dans la littérature, les deux approches (macroscopique et microscopique) pour ce qui est de la prise de décision. En effet, certaines équipes s'intéressent à la décision au niveau de la population. Les modèles d'[Ame et collab. \[2004\]](#); [Halloy et collab. \[2007\]](#) en sont un bon exemple, les chercheurs établissent un ensemble d'équations différentielles relatant l'évolution de la répartition des cafards sous des abris. D'autres équipes se focalisent sur l'émergence de la décision au sein de la population par l'intermédiaires d'agents indépendants et en interaction. C'est d'ailleurs le cas de l'étude menée par [Garnier et collab. \[2009\]](#) qui développe un modèle de prise de décision pour les cafards et l'implémente dans un robot. Ce modèle s'inspire du modèle microscopique développé par [Jeanson et collab. \[2003\]](#) qui reproduit les déplacements de cafards dans une arène circulaire et du modèle macroscopique de [Ame et collab. \[2004\]](#).

Déplacement

Il existe de multiples modèles microscopiques qui décrivent les déplacements collectifs des poissons. Les modèles de particules auto-propulsées (self-propelled particles – SPP – models) s'appuient sur une composante d'évitement des collisions, une composante d'alignement et une autre de cohésion [Couzin et collab. \[2002\]](#); [Lopez et collab. \[2012\]](#). Les modèles de forces sociales (social forces models) considèrent les individus comme des particules newtoniennes assujetties à des forces sociales et physiques qui assurent la cohésion du groupe et l'interaction avec l'environnement [Niwa \[1994, 1996\]](#). D'autres encores, appelés modèles cinétiques, décrivent avec succès l'évolution des trajectoires en utilisant des équations différentielles stochastiques [Gautrais et collab. \[2012, 2009\]](#); [Mwaffo et collab. \[2015\]](#); [Zienkiewicz et collab. \[2015\]](#).

1.4 Références

Abrol, D. P. 2006, «Defensive behaviour of apis cerana f. against predatory wasps», *J Apic Sci*, vol. 50, n° 2, p. 39. [2](#)

Alexander, R. D. 1974, «The evolution of social behavior», *Annual review of ecology and systematics*, p. 325–383. [2](#)

- Altmann, S. A. 1979, «Baboon progressions : order or chaos? a study of one-dimensional group geometry», *Animal Behaviour*, vol. 27, p. 46–80. [14](#)
- Ame, J.-M., C. Rivault et J.-L. Deneubourg. 2004, «Cockroach aggregation based on strain odour recognition», *Animal behaviour*, vol. 68, n° 4, p. 793–801. [8](#), [16](#)
- Anne, O. et E. Rasa. 1983, «Dwarf mongoose and hornbill mutualism in the taru desert, kenya», *Behavioral Ecology and Sociobiology*, vol. 12, n° 3, p. 181–190. [10](#)
- Aristote. *Metaphysica*, vol. X. [8](#)
- Aron, S. et L. Passera. 2009, *Les sociétés animales : évolution de la coopération et organisation sociale*, De Boeck Supérieur. [xv](#), [4](#), [5](#), [10](#)
- Ball, P. 2009, *Shapes : nature's patterns : a tapestry in three parts*, OUP Oxford. [8](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini et collab.. 2008a, «Interaction ruling animal collective behavior depends on topological rather than metric distance : Evidence from a field study», *Proceedings of the national academy of sciences*, vol. 105, n° 4, p. 1232–1237. [5](#), [14](#), [15](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, A. Orlandi, G. Parisi, A. Procaccini, M. Viale et collab.. 2008b, «Empirical investigation of starling flocks : a benchmark study in collective animal behaviour», *Animal behaviour*, vol. 76, n° 1, p. 201–215. [4](#)
- Bell, W. J., L. M. Roth et C. A. Nalepa. 2007, *Cockroaches : ecology, behavior, and natural history*, JHU Press. [4](#)
- Berger, J. 1978, «Group size, foraging, and antipredator ploys : an analysis of bighorn sheep decisions», *Behavioral Ecology and Sociobiology*, vol. 4, n° 1, p. 91–99. [2](#), [7](#)
- Bourjade, M., B. Thierry, M. Hausberger et O. Petit. 2015, «Is leadership a reliable concept in animals? an empirical study in the horse», *PloS one*, vol. 10, n° 5, p. e0126344. [13](#)
- Bourjade, M., B. Thierry, M. Maumy et O. Petit. 2009, «Decision-making in przewalski horses (equus ferus przewalskii) is driven by the ecological contexts of collective movements», *Ethology*, vol. 115, n° 4, p. 321–330. [13](#)
- Bradbury, J. W. et S. L. Vehrencamp. 1998, «Principles of animal communication», . [2](#), [7](#)
- Bret, C. 2014, *Individual determinants of social position and role in group cohesion in three Cercopithecinae species*, Theses, Université de Strasbourg. URL <https://tel.archives-ouvertes.fr/tel-01251567>. [6](#)
- Briard, L., C. Dorn et O. Petit. 2015, «Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses», *Ethology*, vol. 121, n° 9, p. 888–902. [14](#)

- Buhl, J., G. A. Sword et S. J. Simpson. 2012, «Using field data to test locust migratory band collective movement models», *Interface Focus*, p. rfs20120 024. [14](#)
- Bumann, D. et J. Krause. 1993, «Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*)», *Behaviour*, vol. 125, n° 3, p. 189–198. [10](#)
- Camazine, S. 2003, *Self-organization in biological systems*, Princeton University Press. [4](#), [9](#), [16](#)
- Caraco, T. 1979, «Time budgeting and group size : a test of theory», *Ecology*, vol. 60, n° 3, p. 618–627. [2](#)
- Cavagna, A., A. Cimarelli, I. Giardina, G. Parisi, R. Santagati, F. Stefanini et M. Viale. 2010, «Scale-free correlations in starling flocks», *Proceedings of the National Academy of Sciences*, vol. 107, n° 26, p. 11 865–11 870. [5](#)
- Chapman, C. A. et L. J. Chapman. 2000, «Determinants of group size in primates : the importance of travel costs», *On the move : How and why animals travel in groups*, p. 24–42. [2](#)
- Cheney, D. L. et R. M. Seyfarth. 1992, *How monkeys see the world : Inside the mind of another species*, University of Chicago Press. [2](#), [7](#)
- Collignon, B., J. L. Deneubourg et C. Detrain. 2012, «Leader-based and self-organized communication : Modelling group-mass recruitment in ants», *Journal of theoretical biology*, vol. 313, p. 79–86. [10](#)
- Collignon, B. et C. Detrain. 2009, «Distributed leadership and adaptive decision-making in the ant tetramorium caespitum», *Proceedings of the Royal Society of London B : Biological Sciences*, p. rspb20091 976. [10](#)
- Conradt, L. et C. List. 2009, «Group decisions in humans and animals : a survey», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 364, n° 1518, p. 719–742. [11](#), [13](#)
- Conradt, L. et T. J. Roper. 2005, «Consensus decision making in animals», *Trends in ecology & evolution*, vol. 20, n° 8, p. 449–456. [11](#), [13](#)
- Cosnier, J. 1977, «Communication non verbale et langage», *Psychologie médicale*, vol. 9, n° 11, p. 2033–2049. [2](#)
- Côté, I. M. et M. R. Gross. 1993, «Reduced disease in offspring : a benefit of coloniality in sunfish», *Behavioral Ecology and Sociobiology*, vol. 33, n° 4, p. 269–274. [2](#)
- Couzin, I. D., C. C. Ioannou, G. Demirel, T. Gross, C. J. Torney, A. Hartnett, L. Conradt, S. A. Levin et N. E. Leonard. 2011, «Uninformed individuals promote democratic consensus in animal groups», *science*, vol. 334, n° 6062, p. 1578–1580. [12](#)

- Couzin, I. D., J. Krause, N. R. Franks et S. A. Levin. 2005, «Effective leadership and decision-making in animal groups on the move», *Nature*, vol. 433, n° 7025, p. 513–516. [11](#)
- Couzin, I. D., J. Krause, R. James, G. D. Ruxton et N. R. Franks. 2002, «Collective memory and spatial sorting in animal groups», *Journal of theoretical biology*, vol. 218, n° 1, p. 1–11. [16](#)
- Croft, D., B. Arrowsmith, J. Bielby, K. Skinner, E. White, I. D. Couzin, A. Magurran, I. Ramnarine et J. Krause. 2003, «Mechanisms underlying shoal composition in the trinidadian guppy, *poecilia reticulata*», *Oikos*, vol. 100, n° 3, p. 429–438. [6](#), [14](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23 565. [15](#)
- Darwin, C. 1859, *The origin of species*. [2](#)
- Drent, R. et P. Swierstra. 1977, «Goose flocks and food finding : field experiments with barnacle geese in winter», *Wildfowl*, vol. 28, n° 28, p. 6. [3](#)
- Dyer, J. R., A. Johansson, D. Helbing, I. D. Couzin et J. Krause. 2009, «Leadership, consensus decision making and collective behaviour in humans», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 364, n° 1518, p. 781–789. [9](#)
- de Esch, C., H. van der Linde, R. Slieker, R. Willemsen, A. Wolterbeek, R. Woutersen et D. De Groot. 2012, «Locomotor activity assay in zebrafish larvae : influence of age, strain and ethanol», *Neurotoxicology and teratology*, vol. 34, n° 4, p. 425–433. [6](#)
- Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, H. M. Larkin, M.-J. Sellier et D. I. Rubenstein. 2007, «Social relationships and reproductive state influence leadership roles in movements of plains zebra, *equus burchellii*», *Animal Behaviour*, vol. 73, n° 5, p. 825–831. [10](#)
- Fisher, J. et R. A. Hinde. 1949, «The opening of milk bottles by birds», *British Birds*, vol. 42, n° 11, p. 347–357. [4](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [7](#), [8](#)
- Galton, F. 1907, «Vox populi (the wisdom of crowds)», *Nature*, vol. 75, n° 7, p. 450–451. [12](#)
- Garnier, S., J. Gautrais, M. Asadpour, C. Jost et G. Theraulaz. 2009, «Self-organized aggregation triggers collective decision making in a group of cockroach-like robots», *Adaptive Behavior*, vol. 17, n° 2, p. 109–133. [16](#)
- Gautier, J.-P. et A. Gautier-Hion. 1977, «Communication in old world monkeys», . [3](#)
- Gautrais, J., F. Ginelli, R. Fournier, S. Blanco, M. Soria, H. Chaté et G. Theraulaz. 2012, «Deciphering interactions in moving animal groups», *PLoS Comput Biol*, vol. 8, n° 9, p. e1002 678. [16](#)

- Gautrais, J., C. Jost, M. Soria, A. Campo, S. Motsch, R. Fournier, S. Blanco et G. Theraulaz. 2009, «Analyzing fish movement as a persistent turning walker», *Journal of mathematical biology*, vol. 58, n° 3, p. 429–445. [16](#)
- Griebel, G., C. Belzung, G. Perrault et D. J. Sanger. 2000, «Differences in anxiety-related behaviours and in sensitivity to diazepam in inbred and outbred strains of mice», *Psychopharmacology*, vol. 148, n° 2, p. 164–170. [7](#)
- Grünbaum, D., S. Viscido et J. K. Parrish. 2005, «Extracting interactive control algorithms from group dynamics of schooling fish», dans *Cooperative control*, Springer, p. 103–117. [14](#)
- Guayasamin, O. 2013, «Personality matters : A quantitative comparison of asocial and social behaviors in the zebrafish (danio rerio)», . [15](#)
- Halffter, G. 1997, «11• subsocial behavior in scarabaeinae beetles», *The evolution of social behavior in insects and arachnids*, p. 237. [4](#)
- Halloy, J., G. Sempo, G. Caprari, C. Rivault, M. Asadpour, F. Tâche, I. Said, V. Durier, S. Canonge, J. M. Amé et collab.. 2007, «Social integration of robots into groups of cockroaches to control self-organized choices», *Science*, vol. 318, n° 5853, p. 1155–1158. [16](#)
- Harcourt, J. L., T. Z. Ang, G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Social feedback and the emergence of leaders and followers», *Current Biology*, vol. 19, n° 3, p. 248–252. [6](#), [11](#), [14](#), [15](#)
- Herbert-Read, J. 2016, «Understanding how animal groups achieve coordinated movement», *Journal of Experimental Biology*, vol. 219, n° 19, p. 2971–2983. [14](#)
- Herbert-Read, J. E., S. Krause, L. Morrell, T. Schaerf, J. Krause et A. Ward. 2013, «The role of individuality in collective group movement», dans *Proc. R. Soc. B*, vol. 280, The Royal Society, p. 20122564. [15](#)
- Herbert-Read, J. E., A. Perna, R. P. Mann, T. M. Schaerf, D. J. Sumpter et A. J. Ward. 2011, «Inferring the rules of interaction of shoaling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18 726–18 731. [14](#)
- Hoare, D., J. Krause, N. Peuhkuri et J.-G. Godin. 2000, «Body size and shoaling in fish», *Journal of Fish Biology*, vol. 57, n° 6, p. 1351–1366. [4](#), [6](#), [14](#)
- Hockings, K. J., J. R. Anderson et T. Matsuzawa. 2006, «Road crossing in chimpanzees : a risky business», *Current Biology*, vol. 16, n° 17, p. R668–R670. [14](#)
- Holekamp, K. E., E. E. Boydston et L. Smale. 2000, «Group travel in social carnivores.», . [12](#)
- Janson, C. H. et M. S. Di Bitetti. 1997, «Experimental analysis of food detection in capuchin monkeys : effects of distance, travel speed, and resource size», *Behavioral Ecology and Sociobiology*, vol. 41, n° 1, p. 17–24. [2](#), [7](#)

- Jarvis, J. U., M. J. O’Riain, N. C. Bennett et P. W. Sherman. 1994, «Mammalian eusociality : a family affair», *Trends in Ecology & Evolution*, vol. 9, n° 2, p. 47–51. [5](#)
- Jeanson, R., S. Blanco, R. Fournier, J.-L. Deneubourg, V. Fourcassié et G. Theraulaz. 2003, «A model of animal movements in a bounded space», *Journal of Theoretical Biology*, vol. 225, n° 4, p. 443–451. [16](#)
- Jeanson, R., A. Dussutour et V. Fourcassié. 2014, «Key factors for the emergence of collective decision in invertebrates», *Decision-making in invertebrates*, p. 133. [11](#)
- Karihaloo, B. L., K. Zhang et J. Wang. 2013, «Honeybee combs : how the circular cells transform into rounded hexagons», *Journal of The Royal Society Interface*, vol. 10, n° 86, p. 20130299. [8](#)
- Katz, Y., K. Tunstrøm, C. C. Ioannou, C. Huepe et I. D. Couzin. 2011, «Inferring the structure and dynamics of interactions in schooling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18720–18725. [14](#)
- Kenward, R. 1978, «Hawks and doves : factors affecting success and selection in goshawk attacks on woodpigeons», *The Journal of Animal Ecology*, p. 449–460. [2](#)
- King, A. J. 2010, «Follow me! i’m a leader if you do; i’m a failed initiator if you don’t?», *Behavioural Processes*, vol. 84, n° 3, p. 671–674. [9](#)
- Krause, J., D. Hoare, S. Krause, C. Hemelrijk et D. Rubenstein. 2000, «Leadership in fish shoals», *Fish and Fisheries*, vol. 1, n° 1, p. 82–89. [9](#), [10](#), [13](#)
- Krause, J., D. Lusseau et R. James. 2009, «Animal social networks : an introduction», *Behavioral Ecology and Sociobiology*, vol. 63, n° 7, p. 967–973. [10](#)
- Krause, J. et G. D. Ruxton. 2002, *Living in groups*, Oxford University Press. [2](#), [4](#), [6](#), [14](#)
- Lange, M., F. Neuzeret, B. Fabreges, C. Froc, S. Bedu, L. Bally-Cuif et W. H. Norton. 2013, «Inter-individual and inter-strain variations in zebrafish locomotor ontogeny», *PLoS one*, vol. 8, n° 8, p. e70172. [6](#)
- Leblond, C. et S. G. Reebs. 2006, «Individual leadership and boldness in shoals of golden shiners (*notemigonus crysoleucas*)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [14](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [10](#), [14](#)
- Lima, S. L. 1995, «Back to the basics of anti-predatory vigilance : the group-size effect», *Animal Behaviour*, vol. 49, n° 1, p. 11–20. [2](#), [7](#)
- Lopez, U., J. Gautrais, I. D. Couzin et G. Theraulaz. 2012, «From behavioural analyses to models of collective motion in fish schools», *Interface focus*, p. rsfs20120033. [16](#)

- Lukeman, R., Y.-X. Li et L. Edelstein-Keshet. 2010, «Inferring individual rules from collective behavior», *Proceedings of the National Academy of Sciences*, vol. 107, n° 28, p. 12 576–12 580. [14](#)
- Lusseau, D. 2007, «Evidence for social role in a dolphin social network», *Evolutionary ecology*, vol. 21, n° 3, p. 357–366. [10](#)
- Mallon, E., S. Pratt et N. Franks. 2001, «Individual and collective decision-making during nest site selection by the ant *leptothorax albipennis*», *Behavioral Ecology and Sociobiology*, vol. 50, n° 4, p. 352–359. [8](#)
- Manser, M. B., R. M. Seyfarth et D. L. Cheney. 2002, «Suricate alarm calls signal predator class and urgency», *Trends in cognitive sciences*, vol. 6, n° 2, p. 55–57. [2](#), [7](#)
- Mech, L. D. 2012, *Wolf*, Doubleday. [10](#)
- Millot, S., M.-L. Bégout et B. Chatain. 2009, «Risk-taking behaviour variation over time in sea bass *dicentrarchus labrax* : effects of day–night alternation, fish phenotypic characteristics and selection for growth», *Journal of fish biology*, vol. 75, n° 7, p. 1733–1749. [10](#)
- Mwaffo, V., R. P. Anderson, S. Butail et M. Porfiri. 2015, «A jump persistent turning walker to model zebrafish locomotion», *Journal of The Royal Society Interface*, vol. 12, n° 102, p. 20140 884. [16](#)
- Nakayama, S., R. A. Johnstone et A. Manica. 2012, «Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish», *PLoS One*, vol. 7, n° 8, p. e43 747. [10](#)
- Néda, Z., E. Ravasz, Y. Brechet, T. Vicsek et A.-L. Barabási. 2000a, «Self-organizing processes : The sound of many hands clapping», *Nature*, vol. 403, n° 6772, p. 849–850. [8](#)
- Néda, Z., E. Ravasz, T. Vicsek, Y. Brechet et A.-L. Barabási. 2000b, «Physics of the rhythmic applause», *Physical Review E*, vol. 61, n° 6, p. 6987. [8](#)
- Nicolis, G., I. Prigogine et collab.. 1977, *Self-organization in nonequilibrium systems*, vol. 191977, Wiley, New York. [7](#)
- Nieh, J. C. 2010, «A negative feedback signal that is triggered by peril curbs honey bee recruitment», *Current Biology*, vol. 20, n° 4, p. 310–315. [9](#)
- Niwa, H.-S. 1994, «Self-organizing dynamic model of fish schooling», *Journal of theoretical Biology*, vol. 171, n° 2, p. 123–136. [16](#)
- Niwa, H.-S. 1996, «Newtonian dynamical approach to fish schooling», *Journal of Theoretical Biology*, vol. 181, n° 1, p. 47–63. [16](#)
- Oldroyd, B. P., R. S. Gloag, N. Even, W. Wattanachaiyingcharoen et M. Beekman. 2008, «Nest site selection in the open-nesting honeybee *apis florea*», *Behavioral Ecology and Sociobiology*, vol. 62, n° 10, p. 1643–1653. [12](#)

- Pankiw, T. et R. E. Page Jr. 2000, «Response thresholds to sucrose predict foraging division of labor in honeybees», *Behavioral Ecology and Sociobiology*, vol. 47, n° 4, p. 265–267. [6](#)
- Parrish, J. K. et W. M. Hamner. 1997, *Animal groups in three dimensions : how species aggregate*, Cambridge University Press. [4](#)
- Parrish, J. K., S. V. Viscido et D. Grünbaum. 2002, «Self-organized fish schools : an examination of emergent properties», *The biological bulletin*, vol. 202, n° 3, p. 296–305. [8](#)
- Partridge, B. L. 1982, «The structure and function of fish schools», *Scientific american*, vol. 246, n° 6, p. 114–123. [8](#)
- Partridge, B. L., J. Johansson et J. Kalish. 1983, «The structure of schools of giant bluefin tuna in cape cod bay», *Environmental Biology of Fishes*, vol. 9, n° 3-4, p. 253–262. [8](#)
- Partridge, B. L., T. Pitcher, J. M. Cullen et J. Wilson. 1980, «The three-dimensional structure of fish schools», *Behavioral Ecology and Sociobiology*, vol. 6, n° 4, p. 277–288. [15](#)
- Perera, T. B. d. et T. Guilford. 1999, «The orientational consequences of flocking behaviour in homing pigeons, *columba livia*», *Ethology*, vol. 105, n° 1, p. 13–23. [12](#)
- Petit, O. et R. Bon. 2010, «Decision-making processes : the case of collective movements», *Behavioural Processes*, vol. 84, n° 3, p. 635–647. [10](#)
- Petit, O., J. Gautrais, J.-B. Leca, G. Theraulaz et J.-L. Deneubourg. 2009, «Collective decision-making in white-faced capuchin monkeys», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1672, p. 3495–3503. [14](#)
- Pettit, B., Z. Ákos, T. Vicsek et D. Biro. 2015, «Speed determines leadership and leadership determines learning during pigeon flocking», *Current Biology*, vol. 25, n° 23, p. 3132–3137. [10](#)
- Pettit, B., A. Perna, D. Biro et D. J. Sumpter. 2013, «Interaction rules underlying group decisions in homing pigeons», *Journal of the Royal Society Interface*, vol. 10, n° 89, p. 20130529. [14](#)
- Pillot, M.-H., J. Gautrais, P. Arrufat, I. D. Couzin, R. Bon et J.-L. Deneubourg. 2011, «Scalable rules for coherent group motion in a gregarious vertebrate», *PloS one*, vol. 6, n° 1, p. e14487. [14](#)
- Pillot, M. H., J. Gautrais, J. Gouello, P. Michelena, R. Bon et collab.. 2010, «Moving together : Incidental leaders and naïve followers», *Behavioural Processes*, vol. 83, n° 3, p. 235–241. [13](#)
- Powell, G. 1974, «Experimental analysis of the social value of flocking by starlings (*sturnus vulgaris*) in relation to predation and foraging», *Animal Behaviour*, vol. 22, n° 2, p. 501–505. [4](#)
- Pratt, S. C., E. B. Mallon, D. J. Sumpter et N. R. Franks. 2002, «Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *leptothorax albipennis*», *Behavioral Ecology and Sociobiology*, vol. 52, n° 2, p. 117–127. [8](#)

- Pratt, S. C., D. J. Sumpter, E. B. Mallon et N. R. Franks. 2005, «An agent-based model of collective nest choice by the ant *temnothorax albipennis*», *Animal Behaviour*, vol. 70, n° 5, p. 1023–1036. 8
- Rabøl, J. et H. Noer. 1973, «Spring migration in the skylark (*alauda arvensis*) in denmark : Influence of environmental factors on the flocksize and correlation between flocksize and migratory direction», *Vogelwarte*. 12
- Radakov, D. V. 1973, «Schooling in the ecology of fish», . 3
- Ramseyer, A., A. Boissy, B. Dumont et B. Thierry. 2009a, «Decision making in group departures of sheep is a continuous process», *Animal Behaviour*, vol. 78, n° 1, p. 71–78. 13
- Ramseyer, A., B. Thierry, A. Boissy et B. Dumont. 2009b, «Decision-making processes in group departures of cattle», *Ethology*, vol. 115, n° 10, p. 948–957. 13
- Ratcliffe, J. M. et H. M. ter Hofstede. 2005, «Roosts as information centres : social learning of food preferences in bats», *Biology Letters*, vol. 1, n° 1, p. 72–74. 3
- Reebs, S. G. 2000, «Can a minority of informed leaders determine the foraging movements of a fish shoal?», *Animal behaviour*, vol. 59, n° 2, p. 403–409. 4, 10
- Rex, A., U. Sondern, J. Voigt, S. Franck et H. Fink. 1996, «Strain differences in fear-motivated behavior of rats», *Pharmacology Biochemistry and Behavior*, vol. 54, n° 1, p. 107–111. 7
- Rhine, R. J. et R. Tilson. 1987, «Reactions to fear as a proximate factor in the sociospatial organization of baboon progressions», *American Journal of Primatology*, vol. 13, n° 2, p. 119–128. 14
- Robert, T. 1972, «Parental investment and sexual selection», *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York*, p. 136–179. 4
- Robinson, E. J., D. E. Jackson, M. Holcombe et F. L. Ratnieks. 2005, «Insect communication : ‘no entry’ signal in ant foraging», *Nature*, vol. 438, n° 7067, p. 442–442. 9
- Rosenthal, S. B., C. R. Twomey, A. T. Hartnett, H. S. Wu et I. D. Couzin. 2015, «Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion», *Proceedings of the National Academy of Sciences*, vol. 112, n° 15, p. 4690–4695. 10
- Schmitt, R. J. et S. W. Strand. 1982, «Cooperative foraging by yellowtail, *seriola lalandei* (carangidae), on two species of fish prey», *Copeia*, vol. 1982, n° 3, p. 714–717. 2
- Seeley, T. et P. K. Visscher. 2004a, «Group decision making in nest-site selection by honey bees», *Apidologie*, vol. 35, n° 2, p. 101–116. 8
- Seeley, T. D. 2003, «Consensus building during nest-site selection in honey bee swarms : the expiration of dissent», *Behavioral Ecology and Sociobiology*, vol. 53, n° 6, p. 417–424. 11, 13

- Seeley, T. D. et S. C. Buhrman. 1999, «Group decision making in swarms of honey bees», *Behavioral Ecology and Sociobiology*, vol. 45, n° 1, p. 19–31. [8](#), [11](#), [13](#)
- Seeley, T. D., R. H. Seeley et P. Akrotanakul. 1982, «Colony defense strategies of the honeybees in thailand», *Ecological monographs*, vol. 52, n° 1, p. 43–63. [2](#)
- Seeley, T. D. et P. K. Visscher. 2003, «Choosing a home : how the scouts in a honey bee swarm perceive the completion of their group decision making», *Behavioral Ecology and Sociobiology*, vol. 54, n° 5, p. 511–520. [9](#)
- Seeley, T. D. et P. K. Visscher. 2004b, «Quorum sensing during nest-site selection by honeybee swarms», *Behavioral Ecology and Sociobiology*, vol. 56, n° 6, p. 594–601. [9](#)
- Séguret, A., B. Collignon et J. Halloy. 2016, «Strains differences in the collective behaviour of zebrafish (danio rerio) in heterogeneous environment», *Royal Society open science*, vol. 3, n° 1, p. 160451. [7](#), [15](#)
- Silk, M. J., D. P. Croft, T. Tregenza et S. Bearhop. 2014, «The importance of fission–fusion social group dynamics in birds», *Ibis*, vol. 156, n° 4, p. 701–715. [5](#)
- Simons, A. M. 2004, «Many wrongs : the advantage of group navigation», *Trends in ecology & evolution*, vol. 19, n° 9, p. 453–455. [12](#)
- Stewart, K. J. et A. H. Harcourt. 1994, «Gorillas' vocalizations during rest periods : signals of impending departure?», *Behaviour*, vol. 130, n° 1, p. 29–40. [12](#)
- Street, N. et P. Hart. 1985, «Group size and patch location by the stoneloach, *noemacheilus barbatus*, a non-visually foraging predator», *Journal of fish biology*, vol. 27, n° 6, p. 785–792. [2](#)
- Struhsaker, T. T. 1981, «Polyspecific associations among tropical rain-forest primates», *Zeitschrift für Tierpsychologie*, vol. 57, n° 3-4, p. 268–304. [2](#)
- Sueur, C., A. J. King, L. Conradt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C. M. Schaffner, L. Williams, D. Zinner et F. Aureli. 2011, «Collective decision-making and fission–fusion dynamics : a conceptual framework», *Oikos*, vol. 120, n° 11, p. 1608–1617. [6](#)
- Sueur, C. et O. Petit. 2008, «Shared or unshared consensus decision in macaques?», *Behavioural Processes*, vol. 78, n° 1, p. 84–92. [10](#), [11](#)
- Sumpter, D. J. 2006, «The principles of collective animal behaviour», *Philosophical Transactions of the Royal Society B : Biological Sciences*, vol. 361, n° 1465, p. 5–22. [9](#)
- Sumpter, D. J. 2010, *Collective animal behavior*, Princeton University Press. [2](#), [16](#)
- Sumpter, D. J. et S. C. Pratt. 2009, «Quorum responses and consensus decision making», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 364, n° 1518, p. 743–753. [8](#)

- Van Schaik, C. P., M. A. Van Noordwijk, B. Warsono et E. Sutriyono. 1983, «Party size and early detection of predators in sumatran forest primates», *Primates*, vol. 24, n° 2, p. 211–221. [2](#)
- Wallraff, H. G. 1978, «Social interrelations involved in migratory orientation of birds : possible contribution of field studies», *Oikos*, p. 401–404. [12](#)
- Ward, A. J., D. J. Sumpter, I. D. Couzin, P. J. Hart et J. Krause. 2008, «Quorum decision-making facilitates information transfer in fish shoals», *Proceedings of the National Academy of Sciences*, vol. 105, n° 19, p. 6948–6953. [9](#), [13](#)
- Watts, D. 2000, «Mountain gorilla habitat use strategies and group movements», *On the move : how and why animals travel in groups*. University of Chicago Press, Chicago, IL, p. 351–374. [10](#)
- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. Tutin, R. W. Wrangham et C. Boesch. 1999, «Cultures in chimpanzees», *Nature*, vol. 399, n° 6737, p. 682–685. [4](#)
- Wilson, E. O. 2000, *Sociobiology*, Harvard University Press. [5](#)
- Zienkiewicz, A., D. A. Barton, M. Porfiri et M. di Bernardo. 2015, «Data-driven stochastic modelling of zebrafish locomotion», *Journal of mathematical biology*, vol. 71, n° 5, p. 1081–1105. [16](#)
- Zuberbühler, K. 2001, «Predator-specific alarm calls in campbell's monkeys, *cercopithecus campbelli*», *Behavioral Ecology and Sociobiology*, vol. 50, n° 5, p. 414–422. [2](#), [7](#)

Chapitre 2

Objectifs

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2.1 Objectifs de la thèse

Les objectifs principaux de la thèse sont de créer un système expérimental de grande taille, non biaisé, facilement reproductible et pouvant accueillir des éléments perturbateurs afin d'étudier, en milieux complexes, l'influence des mécanismes de cohésion et de prise de décision collective sur les groupes de poissons. Cette thèse étant financée par le projet européen ASSISI, notre équipe de recherche a pour but de développer un modèle multi-agent des comportement collectifs de zebrafish (*Danio rerio*). Ainsi, nous analysons, tant au niveau individuel que collectif, les déplacements des zebrafish dans des contextes environnementaux qui ne sont pas sans évoquer la réalité de leur habitat et implémentons nos découvertes dans le modèle. Nous utilisons, de ce fait, une approche expérimentale permettant d'observer ces mécanismes.

Nous répondrons, en particulier, aux questions suivantes :

1. Comment le groupe s'organise-t-il quand il est confronté à des choix binaires? Les zebrafish prennent-ils des décisions collectives? Existe-il des événements déclencheurs de la prise de décision? Quels sont les dynamiques de la prise de décision?
2. Les différences comportementales observées au niveau individuel entre deux souches de la même espèce *Danio rerio* ont-elles des répercussions au niveau collectif? Quels mécanismes sont impliqués dans ces différences de comportements collectifs? D'autres facteurs agissent-ils sur la cohésion du groupe?

3. Comment les structures de groupes s'adaptent-elles aux variations de densité de ces mêmes groupes? Autour de quels mécanismes sociaux les groupes s'organisent-ils? Quel est l'impact de la pression du groupe sur ces mécanismes?

2.2 Objectifs du projet européen ASSISI

Le but du projet est d'établir une société de robots capables de développer des canaux de communication entre des sociétés d'animaux (abeilles et zebrafish), et ce de façon autonome. Grâce à des algorithmes d'évolution, les robots s'adaptent et apprennent à interagir avec les animaux. Les principaux objectifs du projet ASSISI sont listés ici (en gras, les points sur lesquels j'ai travaillé) :

1. Développer des robots pouvant influencer les comportements collectifs d'abeilles et de poissons.
2. **Établir une société adaptative, auto-organisée et mixte de robots et d'animaux.**
3. Permettre aux robots d'apprendre de façon autonome le langage social des animaux.
4. **Établir des sociétés mixtes poursuivant un même objectif, défini par l'humain.**
5. **Permettre aux robots de gagner de nouvelles compétences en implémentant les capacités des animaux (sensitives, cognitives, ...)**

Chapitre 3

Matériel et méthodes

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3.1 Présentation de l'espèce

Danio rerio (zebrafish) est un poisson d'eau douce de la famille des Cyprinidés, de petite taille (3.5 à 4.5 cm). Originaires d'Inde, les zebrafish sont diurnes. Leur habitat est très varié et s'étend de simples rivières peu profondes et au courant faible à des étangs non permanents voire même des canaux d'irrigation. Ces poissons sont très robustes et s'accommodent de températures d'eau très variable allant de 6°C en hivers à 38°C lors de l'été (Spence et collab. [2008]).

Danio rerio est omnivore. Son régime alimentaire comprend principalement du zooplancton et des insectes mais il lui arrive parfois de ne se nourrir de phytoplanctons, d'algues, de détritrus, de sable, d'écailles de poissons et autres oeufs d'invertébrés, ... (Dutta [1993]; McClure et collab. [2006]; Spence et collab. [2007])

Les zebrafish sont ovipares. Tous les deux à trois jours, selon l'âge, les femelles peuvent pondre plusieurs centaines d'oeufs à la fois. En moyenne, les zebrafish atteignent leur maturité 75 jours après la fécondation (Spence et collab. [2008]).

Facilité d'élevage, robustesse, ponte gigantesque et maturité rapide ont fait de ce poisson un candidat de choix pour les laboratoires de recherche. Il est, aujourd'hui, un organisme modèle (Norton et Bally-Cuif [2010]; Oliveira [2014]) et a été en 2013 entièrement séquencé (Howe et collab. [2013]). Il existe une multitude de souches de zebrafish, aux propriétés génétiques et phénotypiques variées, utilisées en fonction des besoins de la recherche, en cancérologie, en neurologie, en toxicologie (Egan et collab. [2009]), etc.



FIGURE 3.1 – Groupe de *Danio rerio* de type AB. ©LSRO EPFL

Enfin, les zebrafish sont grégaires. Ils vivent en bancs de tailles très variables, de quelques individus à plusieurs centaines selon la région, la qualité de l'eau ou les paramètres environnementaux. Malgré sa très forte présence dans les laboratoires et des études comportementales en nombre, *Danio rerio* est l'objet de recherche sur ses comportements collectifs

depuis peu (Miller et Gerlai [2007, 2011]).

3.2 Élevage

Nous élevons principalement, dans notre animalerie, deux souches de *Danio rerio* : AB et TL. La souche AB présente une peau zébrée et de courtes nageoires alors que la souche TL a une peau léopard et de longues nageoires. La souche AB, apparue en 1991, est issue du croisement des souches A et B. La souche TL, elle, est homozygote pour les gènes leo^{t1} , mutation récessive causant l'apparition de points sur la peau de l'adulte and lof^{dt2} responsable de l'apparition des longues nageoires (Iovine et Johnson [2000], Watanabe et collab. [2006]).

Les poissons élevés dans notre animalerie sont issus de deux centres de recherche parisiens : l'Institut Curie et l'Institut du Cerveau et de la Moelle Épinière. Nous procédons à des reproductions plusieurs fois par mois afin de re-constituer le pool nécessaire de zebrafish pour nos expériences. Plusieurs générations se sont depuis succédées.

Nous avons mis en place un système d'élevage automatisé (ZebTEC rack distribué par Tecniplast) composé de 50 bacs d'élevage de 3.5L (28 cm x 17 cm x 10 cm) (3.2). Il est connecté à un osmoseur qui fournit quotidiennement de l'eau osmosée à $27 \mu\text{S}/\text{cm}^2$. Nous élevons dans chaque bac d'élevage 20 zebrafish. La température est fixée 27°C , la salinité à $500 \mu\text{S}/\text{cm}^2$, le pH à 7.5 et le taux de nitrites est inférieur à $0.3\text{mg}/\text{L}$. L'eau est renouvelée automatiquement de 10% par heure. Les poissons sont nourris deux fois par jour, semaine et week-end, à heure régulière, avec de la nourriture spécialisée (Special Diets Services SDS-400 Scientific Fish Food). Nous avons imposé un cycle jour nuit avec éclairage automatique : de 9h à 19h la lumière est allumée.



FIGURE 3.2 – Élevage automatisé.

3.3 Système expérimental

L'aquarium d'expérience mesure 1.2 m x 1.2 m x 0.2 m et est confiné dans une zone expérimentale de 2 m x 2 m x 2.35 m recouverte de tissu blanc 3.3. L'idée étant d'isoler les expériences et d'homogénéiser la luminosité. Au-dessus de la zone expérimentale, fixée au plafond, une caméra à haute résolution (2048 x 2048 px, Basler Scout aca2040-25gm) filme les expériences à quinze images par seconde. Elle est connectée à un ordinateur via son port rj-45. La luminosité est assurée par quatre lampes LED de 33W (LED LP-500U, température de couleur : 5500K à 6000K), positionnées à chaque coin de l'aquarium, au-dessus du niveau de l'eau et dirigées vers le tissu.

L'eau de l'aquarium expérimental est issue d'un système de production d'eau aux paramètres contrôlés et identiques à l'eau d'élevage (température à 27°C, salinité à 500 μ S/cm², pH à 7.5 et taux de nitrites inférieur à 0.3mg/L). Ceci afin de minimiser le stress des poissons.

Nous avons dupliqué notre système expérimental afin de multiplier les expériences.



FIGURE 3.3 – Système expérimental avec l'aquarium surélevé, le drap isolant et la caméra qui surplombe.

3.4 Expérience, analyse de données et tests statistiques

Lors de nos expériences, nous façonnons l'environnement des zebrafish à l'aide de divers matériaux, de différentes formes. Lors de l'étude sur les points de repères (landmarks) nous avons utilisé des disques bleus transparents en plexiglas et des cylindres en plastiques recouverts de rubans adhésifs jaune et vert. Pour l'étude des départs collectifs, nous avons conçu, sur des logiciels de conception assistée par ordinateur (CAO), et découpé, sur des machines de découpe laser, des plaques de poly(méthacrylate de méthyle) de 0.003 m d'épaisseur. Elles ont ensuite été assemblées afin de former le "labyrinthe" souhaité : deux chambres de 0.3 m x 0.3 m x 0.14 m connectées entre elles par un long couloir de 0.57 m x 0.1 m x 0.14 m. D'autres formes ont été créées : un labyrinthe en Y de trois chambres connectées entre elle par trois couloirs se rejoignant au centre, une "matrice" de 4 x 4 chambres avec des connexions entre chaque chambres.

Pour chaque expérience, nous sélectionnons au hasard les poissons à tester et quelque soit leur genre. Ceux-ci ne sont testés qu'une seule fois afin d'éviter tout apprentissage. Les poissons sont alors déposés dans l'aquarium expérimental à l'aide d'une épuisette dans un cylindre en plexiglas transparent. Après une période d'acclimatation de cinq mi-

minutes, le cylindre est retiré et l'expérience commence. Après 66 minutes, soit 60000 images enregistrées, l'expérience est arrêtée et les poissons retournent dans un bac d'élevage. Le système expérimental est à nouveau prêt pour accueillir de nouveaux sujets.

La vidéo enregistrée est traquée hors ligne par le logiciel idTracker (Pérez-Escudero et collab. [2014]). Ce logiciel nous fournit la position et l'identité des poissons à chaque pas de temps. Au final, nous aurons un fichier .txt des positions des poissons avec leur identité. Nous prélevons alors les 54000 dernières positions de ces fichiers afin de ne travailler que sur une heure. Les expériences sont renouvelées de dix à douze fois, et ce afin d'obtenir des résultats statistiques tangibles.

Les analyses de données sont effectuées sous le langage de programmation Python, avec l'aide de certaines bibliothèques (numpy, pylab, scilab et matplotlib), les analyses statistiques sont effectuées en Python et en Matlab®.

3.5 Références

- Dutta, S. 1993, «Food and feeding habits of danio rerio(ham. buch) inhabiting gadigarh stream, jammu», *Journal of Freshwater Biology*, vol. 5, n° 2, p. 165–168. [30](#)
- Egan, R. J., C. L. Bergner, P. C. Hart, J. M. Cachat, P. R. Canavello, M. F. Elegante, S. I. Elkhayat, B. K. Bartels, A. K. Tien, D. H. Tien et collab.. 2009, «Understanding behavioral and physiological phenotypes of stress and anxiety in zebrafish», *Behavioural brain research*, vol. 205, n° 1, p. 38–44. [30](#)
- Howe, K., M. D. Clark, C. F. Torroja, J. Torrance, C. Berthelot, M. Muffato, J. E. Collins, S. Humphray, K. McLaren, L. Matthews et collab.. 2013, «The zebrafish reference genome sequence and its relationship to the human genome», *Nature*, vol. 496, n° 7446, p. 498–503. [30](#)
- Iovine, M. K. et S. L. Johnson. 2000, «Genetic analysis of isometric growth control mechanisms in the zebrafish caudal fin», *Genetics*, vol. 155, n° 3, p. 1321–1329. [31](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danio-nin fishes, including the zebrafish danio rerio», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [30](#)
- Miller, N. et R. Gerlai. 2007, «Quantification of shoaling behaviour in zebrafish (danio rerio)», *Behavioural brain research*, vol. 184, n° 2, p. 157–166. [31](#)
- Miller, N. Y. et R. Gerlai. 2011, «Shoaling in zebrafish : what we don't know», *Reviews in the Neurosciences*, vol. 22, n° 1, p. 17–25. [31](#)
- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [30](#)

- Oliveira, R. F. 2014, «Mind the fish : zebrafish as a model in cognitive social neuroscience», *Frontiers in neural circuits*. 30
- Pérez-Escudero, A., J. Vicente-Page, R. C. Hinz, S. Arganda et G. G. De Polavieja. 2014, «idtracker : tracking individuals in a group by automatic identification of unmarked animals», *Nature methods*, vol. 11, n° 7, p. 743–748. 34
- Spence, R., M. Fatema, S. Ellis, Z. Ahmed et C. Smith. 2007, «Diet, growth and recruitment of wild zebrafish in bangladesh», *Journal of Fish Biology*, vol. 71, n° 1, p. 304–309. 30
- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, danio rerio», *Biological Reviews*, vol. 83, n° 1, p. 13–34. 30
- Watanabe, M., M. Iwashita, M. Ishii, Y. Kurachi, A. Kawakami, S. Kondo et N. Okada. 2006, «Spot pattern of leopard danio is caused by mutation in the zebrafish connexin41. 8 gene», *EMBO reports*, vol. 7, n° 9, p. 893–897. 31

Chapitre 4

Projet ASSISI|bf

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4.1 Le projet

Les Systèmes Collectifs Adaptatifs (Collective Adaptive Systems – CAS) sont des ensembles constitués d'un grand nombre d'unités en interaction capables de s'adapter à leur environnement par l'apprentissage. Ce sont les théories mathématiques s'appuyant sur les analyses d'écosystèmes naturels, des systèmes sociaux et autres systèmes complexes d'interactions physiques qui ont donné naissance aux CAS. Théorie de l'information (Pierce [2012]; Wiener [1961]), théorie des systèmes non-linéaires (Nicolis et collab. [1977]), cybernétique (Wiener [1961]), auto-organisation (Camazine et collab. [2001]), systèmes dynamiques (Forrester et Forrester [1971]) sont autant de champs de recherche dans lesquels la recherche sur les CAS pioche sans toutefois réussir à les rassembler. Le projet ASSISI|BF cherche à relever ce challenge. Les CAS du projet, comme les CAS naturels, se doivent d'être suffisamment robustes pour perdurer dans le monde réel, flexibles pour se sortir de situations inattendues, exploitables afin de répondre à toutes les demandes de l'utilisateur, exploratoires, évolutifs afin de l'utiliser dans des problèmes de plus grande ampleur et bien sûr simple à construire et à produire en masse. L'idée est donc de faire interagir des sociétés animales (de poissons à l'université Paris Diderot ou d'abeilles à UNI Graz) avec des sociétés de robots. La création de telles sociétés mixtes se fonde sur les analyses des comportements individuels et en groupes des animaux : types de déplacement, vitesse, accélération, cohésion, motifs comportementaux, sous-groupes, préférences, etc. Une fois ces données récupérées et retranscrites sous forme de modèles multi-agents, elles seront implémentées dans les robots qui pourront alors reproduire les faits et gestes des animaux étudiés et interagir avec eux.

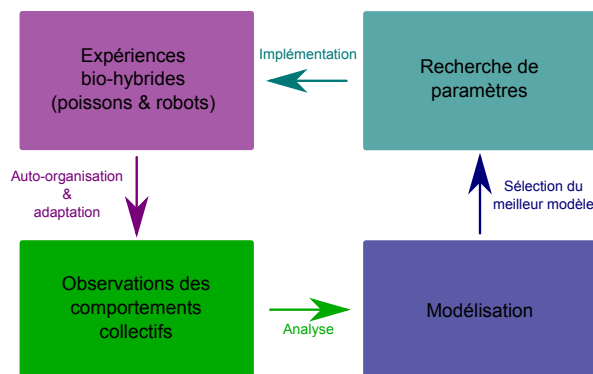


FIGURE 4.1 – Créer une société mixte de poissons et de robots.

4.2 Des robots pour l'éthologie

Comprendre et interagir avec des animaux ou des sociétés animales n'est pas récent. Avant le développement de l'élevage et la domestication, les êtres humains poursuivaient

leurs proies, apprenaient leurs démarches et leurs régimes alimentaires, et se rapprochant au plus près d'eux maximisaient leur chance de capture. Dans *The study of instinct*, Tinbergen [1951] remarque qu'il est possible d'interagir avec les animaux qu'il étudie et de déclencher les comportements attendus en façonnant des stimuli nécessaires et suffisants. Ainsi, il remarque que les épinoches mâles, poissons territoriaux et au ventre teinté en rouge en période de reproduction, s'attaquent à tout intrus pénétrant leurs territoires. Il présente dès lors un leurre mâle réaliste et non coloré ou un leurre grossier et coloré en rouge sur sa partie ventrale et constate que les mâles attaquent plus vigoureusement les leurres grossiers et colorés. De même, il réalise une expérience avec de jeunes goélands argentés (*Larus Argentatus*) où il montre qu'un simple bâton piquant le sol et présentant certaines caractéristiques nécessaires et suffisantes, déclenche des motifs comportementaux similaires à ceux déclenchés par la mère, elle-même, piquant le sol. On parle ici de schème d'action spécifique.

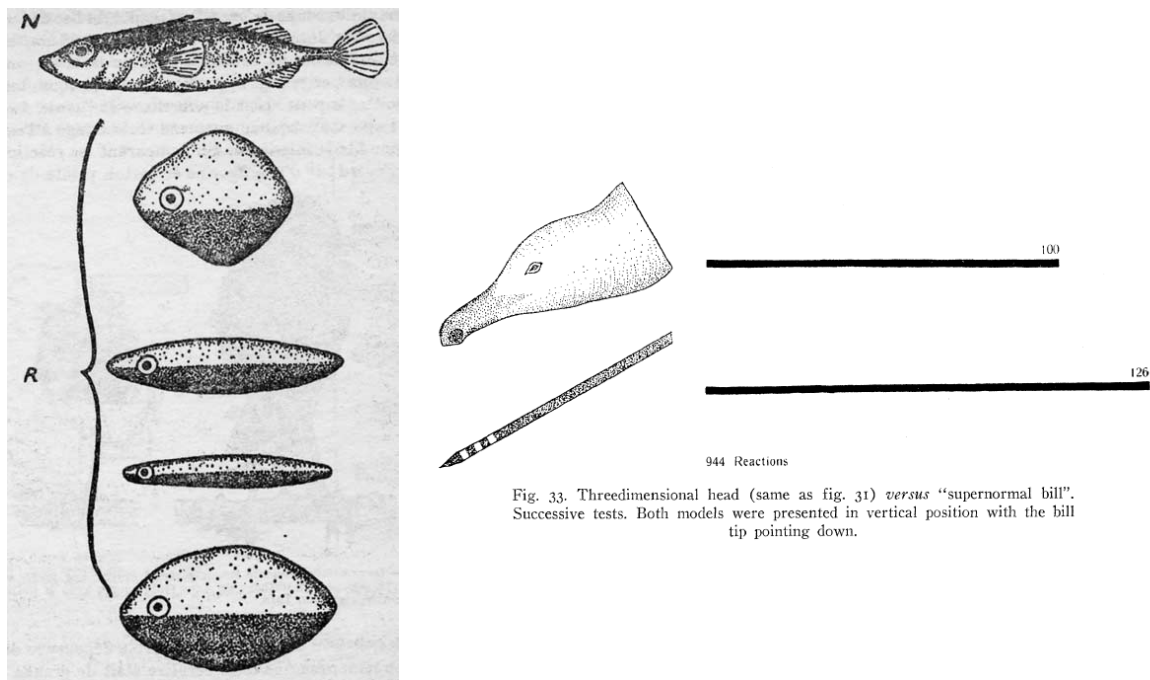


FIGURE 4.2 – Stimuli façonnés par Tinbergen [1951] pour *The study of instinct*.

C'est Tinbergen [1963] qui définit les fondements de l'éthologie autour de quatre questions fondamentales. Ainsi, les comportements doivent être étudiés sous ces quatre aspects :

1. La *causalité* : quels facteurs internes ou externes déclenchent un comportement ?
2. La *fonction* : quelle est la fonction du comportement ?
3. L'*ontogenèse* : comment le comportement se met en place au cours du développement de l'individu ?
4. La *phylogenèse* : comment le comportement est apparu aux de l'évolution ?

En s’inspirant de ces recherches et vu l’évolution des techniques et des technologies, il est aujourd’hui possible d’apporter un vent nouveau à l’éthologie et de quantifier au plus haut point les comportements individuels et collectifs, en s’aidant de robots modulaires et intelligents implémentant des modèles comportementaux de plus en plus réalistes. Depuis une dizaine d’année, les chercheurs mettent au point des robots toujours plus perfectionnés qui arrivent à créer le lien avec les espèces étudiées. Halloy et collab. [2007] ont développé une société bio-hybride de cafards et de robots cafards, Abaid et collab. [2012]; Faria et collab. [2010] font interagir un poisson robot avec des zebrafish ou des épinoches.

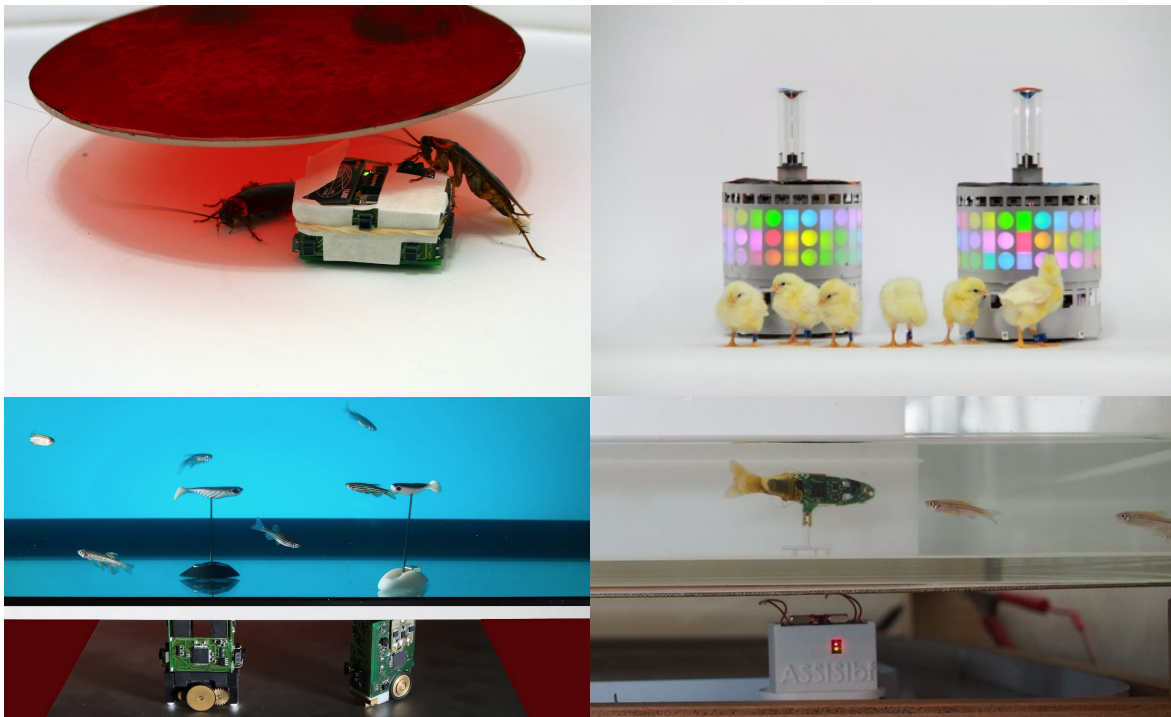


FIGURE 4.3 – Exemples de sociétés bio-hybrides. Crédit photo : José Halloy, Conny Lee

4.3 Références

- Abaid, N., T. Bartolini, S. Macrì et M. Porfiri. 2012, «Zebrafish responds differentially to a robotic fish of varying aspect ratio, tail beat frequency, noise, and color», *Behavioural brain research*, vol. 233, n° 2, p. 545–553. 40
- Camazine, S., J.-L. Deneubourg, N. R. Franks, J. Sneyd, G. Theraulaz et E. Bonabeau. 2001, «Self-organizing biological systems», . 38
- Faria, J. J., J. R. Dyer, R. O. Clément, I. D. Couzin, N. Holt, A. J. Ward, D. Waters et J. Krause. 2010, «A novel method for investigating the collective behaviour of fish : introducing ‘robofish’», *Behavioral Ecology and Sociobiology*, vol. 64, n° 8, p. 1211–1218. 40

Forrester, J. W. et J. W. Forrester. 1971, *World dynamics*, vol. 59, Wright-Allen Press Cambridge, MA.

38

Halloy, J., G. Sempo, G. Caprari, C. Rivault, M. Asadpour, F. Tâche, I. Said, V. Durier, S. Canonge, J. M. Amé et collab.. 2007, «Social integration of robots into groups of cockroaches to control self-organized choices», *Science*, vol. 318, n° 5853, p. 1155–1158. 40

Nicolis, G., I. Prigogine et collab.. 1977, *Self-organization in nonequilibrium systems*, vol. 191977, Wiley, New York. 38

Pierce, J. R. 2012, *An introduction to information theory : symbols, signals and noise*, Courier Corporation. 38

Tinbergen, N. 1951, «The study of instinct.», . xi, 39

Tinbergen, N. 1963, «On aims and methods of ethology», *Zeitschrift für Tierpsychologie*, vol. 20, n° 4, p. 410–433. 39

Wiener, N. 1961, *Cybernetics or Control and Communication in the Animal and the Machine*, vol. 25, MIT press. 38

Chapitre 5

Strain differences in the collective behaviour of zebrafish (*Danio rerio*) in heterogeneous environment

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5.1 Résumé

De récentes études ont montré des différences dans les déplacements individuels et collectifs chez des souches de la même espèce. Ici, nous analysons les déplacements collectifs et les réponses à des stimuli visuels de deux souches de zebrafish (AB et TL) morphologiquement différentes. Nous observons pendant une heure dix populations différentes de cinq et dix individus de chaque souche dans un grand aquarium expérimental. Il a été positionné à l'intérieur de ce dernier deux repères identiques caractérisés par soit des cylindres, soit des disques. Nous traquons ainsi les positions des poissons et développons des outils d'analyse des comportements du groupe. À première vue, les deux souches évitent les zones à découvert et préfèrent nager à proximité des murs de l'aquarium et des repères. La souche AB se trouve plus souvent à proximité des repères que la souche TL et chacune d'entre elle transite entre les deux repères sans marquer de préférence ni pour l'un ni pour l'autre. Enfin, la souche TL est plus cohésive que la souche AB. Ainsi, l'hétérogénéité de l'environnement et la durée des expériences nous ont permis de révéler les différences comportementales individuelles et collectives entre deux souches de zebrafish. Ces résultats apportent de nouvelles informations quant à la nécessité de prendre en considération les différences entre les souches de zebrafish lors d'études sur leurs comportements collectifs.

5.2 Abstract

Recent studies show differences in individual motion and shoaling tendency between strains of the same species. Here, we analyse collective motion and response to visual stimuli in two morphologically different strains (TL and AB) of zebrafish. For both strains, we observed 10 groups of 5 and 10 zebrafish swimming freely in a large experimental tank with two identical landmarks (cylinders or disks) for one hour. We tracked the positions of the fish by an automated tracking method and compute several metrics at the group level. First, the probability of presence shows that both strains avoid free space and are more likely to swim in the vicinity of the walls of the tank and the landmarks. Second, the analysis of landmarks occupancy shows that AB zebrafish are more present in their vicinity than TL ones and that both strains regularly transit from one to the other one with no preference on the long duration. Finally, TL zebrafish show a higher cohesion than AB zebrafish. Thus, environmental heterogeneity and duration of the trials allow to reveal individual and collective behavioural variabilities among different strains of zebrafish. These results provide a new insight into the need to take into account individual variability of zebrafish strains for studying collective behaviour.

5.3 Introduction

Collective decision making has been evidenced in many animal species and contexts [Sumpter et collab. \[2012\]](#) including food collection [Detrain et Deneubourg \[2008\]](#), problem-solving [Dussutour et collab. \[2009\]](#); [Jeanson et collab. \[2014\]](#), collective movement [Engeszer et collab. \[2007\]](#); [Hemelrijk et Hildenbrandt \[2012\]](#); [Herbert-Read et collab. \[2011\]](#); [Parrish et collab. \[2002\]](#); [Petit et Bon \[2010\]](#); [Radakov \[1973\]](#); [Sueur et collab. \[2011\]](#) or nest site selection [Amé et collab. \[2006\]](#); [Franks et collab. \[2002\]](#). In this latter case, social animals have to select a resting site among several potential options in a complex environment. This selection can be made either through individual decisions or complex decision-making processes involving the participation of all individuals [Conradt et Roper \[2005\]](#) and can be temporary or permanent according to the needs and living style of the considered species.

This process of collective decision has been studied for a long time in social animals that select a permanent home : social insects, fish and birds. In particular, experiments on fish have been generally designed to observe preferences for particular environmental features or landmarks during a relatively short experimental time (few seconds [Ward et collab. \[2011\]](#), 5 minutes [Sison et Gerlai \[2010\]](#), 10 minutes [Miller et collab. \[2013\]](#), up to 30 minutes per trial [Kistler et collab. \[2011\]](#)). These studies have shown for example that landmarks in a bare tank arouse interest and attract the fish [Kistler et collab. \[2011\]](#); [Sullivan et collab. \[2016\]](#) and that variations of the shape of these landmarks can change territory features [Suriyampola et Eason \[2014, 2015\]](#).

While these studies provide numerous insights on the individual and collective preferences in fish groups, they generally rely on the comparison between two or more qualitatively different alternatives. Thus, the selection of one option is often based on an intrinsic preference for a particular feature in comparison with the others. Such asymmetric choices may hide the collective decision that results from the internal processes of decision-making of the group.

Furthermore, it has been evidenced with fish (*Oreochromis niloticus*, *Gambusia holbrooki*, *Notemigonus crysoleucas*) that the group sizes impact motion [Becco et collab. \[2006\]](#); [Herbert-Read et collab. \[2013\]](#) (speed, turning speed and nearest neighbour distance) and some moving behaviours [Tunstrøm et collab. \[2013\]](#) as the milling and the alignment. Depending on the species, studies show opposite results : [Becco et collab. \[2006\]](#) works with *Oreochromis niloticus* with two group sizes (330 and 905 fish) ; [Tunstrøm et collab. \[2013\]](#) works with *Notemigonus crysoleucas* with four group sizes (30, 70, 150 and 300 fish). Increasing the group size of *Oreochromis niloticus*, makes stronger alignments when for *Notemigonus crysoleucas* alignments decrease. In this study, we test whether and how collective behaviours and decision-making are affected by the strain and the group sizes.

Here, our aim is to characterise the collective behaviour of groups of zebrafish swimming in an environment with identical landmarks. We observe the collective motion of small shoals of different group sizes (5 and 10 fish) and of two different zebrafish strains (laboratory wild type AB or TL). Zebrafish are a gregarious vertebrate model organism that can be used to study the cohesion of the group and its decision-making Norton et Bally-Cuif [2010]; Oliveira [2014]. Originating from India the zebrafish is a diurnal species that prefers staying in groups both in nature and in the laboratory Engeszer et collab. [2007]; McClure et collab. [2006]; Spence et collab. [2008]. There is a wide variability in shoal sizes : zebrafish live in small groups in shallow freshwaters Parichy [2015]; Pritchard et collab. [2001] and can aggregate into larger groups of 300 individuals Suriyampola et collab. [2016]. Zebrafish living in a variety of habitats with varying structural complexities Aru; Suriyampola et collab. [2016] (from river channels, irrigation canals to beels), we set our experimental method relying on the observations of fish freely swimming in an open environment along with heterogeneous landmarks rather than in a constraining set-up (i.e. mazes as used in Miller et collab. [2013]; Sison et Gerlai [2010]; Ward et collab. [2011]). We observe during one hour per replicate each group of fish swimming in a large experimental tank (1mx1m and 1.20mx1.20m) with two spots of interest (landmarks).

The landmarks consist of two striped yellow-green opaque plastic cylinders placed in the water column or two blue transparent floating Perspex disks providing shadow. We choose these colours in the visible spectrum of the zebrafish according to the results of Risner et collab. [2006]. We expect that these landmarks placed in a homogeneous environment could induce a choice of one preferred option by the zebrafish as evidenced for other species faced with identical resources Amé et collab. [2006]; Beckers et collab. [1992, 1990]. On the one hand, we test with cylinders the effect of visual and physical cues in the water column on collective choices. Since zebrafish are known to swim along the walls of the experimental tank Collignon et collab. [2016], cylinders could act as such walls in the water column. On the other hand, we test with floating disks the impact of visual and physical cues above water, on collective choices. We placed disks and cylinders as landmarks to see whether and how the two strains of zebrafish will adapt their group behaviour and their preferences for landmarks.

5.4 Results

5.4.1 Differences of group features between AB and TL strains of zebrafish

We test two types of landmarks : striped yellow and green cylinders and floating perspex transparent blue disks (see Methods), on two laboratory strains of zebrafish (TL and

AB) for 10 replicates. We computed the interindividual distances between all fish to characterize the cohesion of the group for both strains and group sizes in the presence of the cylinders. The distribution of all interindividual distances (Figure 5.1) shows that the groups of TL zebrafish have a stronger cohesion (5 TL : Median = 0.12m and 10 TL : Median = 0.14m) than the groups of AB zebrafish (5 AB : Median = 0.27m and 10 AB : Median = 0.23m). The intra-strain comparison for the two group sizes shows that the distribution significantly differs from each other (Kolmogorov-Smirnov test, 5 AB vs 10 AB, $D = 0.102$, $p < 0.001$; 5 TL vs 10 TL, $D = 0.080$, $p < 0.001$). The inter-strain comparison for similar group sizes also reveals a statistical difference between the distributions (Kolmogorov-Smirnov test, 10 AB vs 10 TL, $D = 0.184$, $p < 0.001$; 5 AB vs 5 TL, $D = 0.161$, $p < 0.001$).

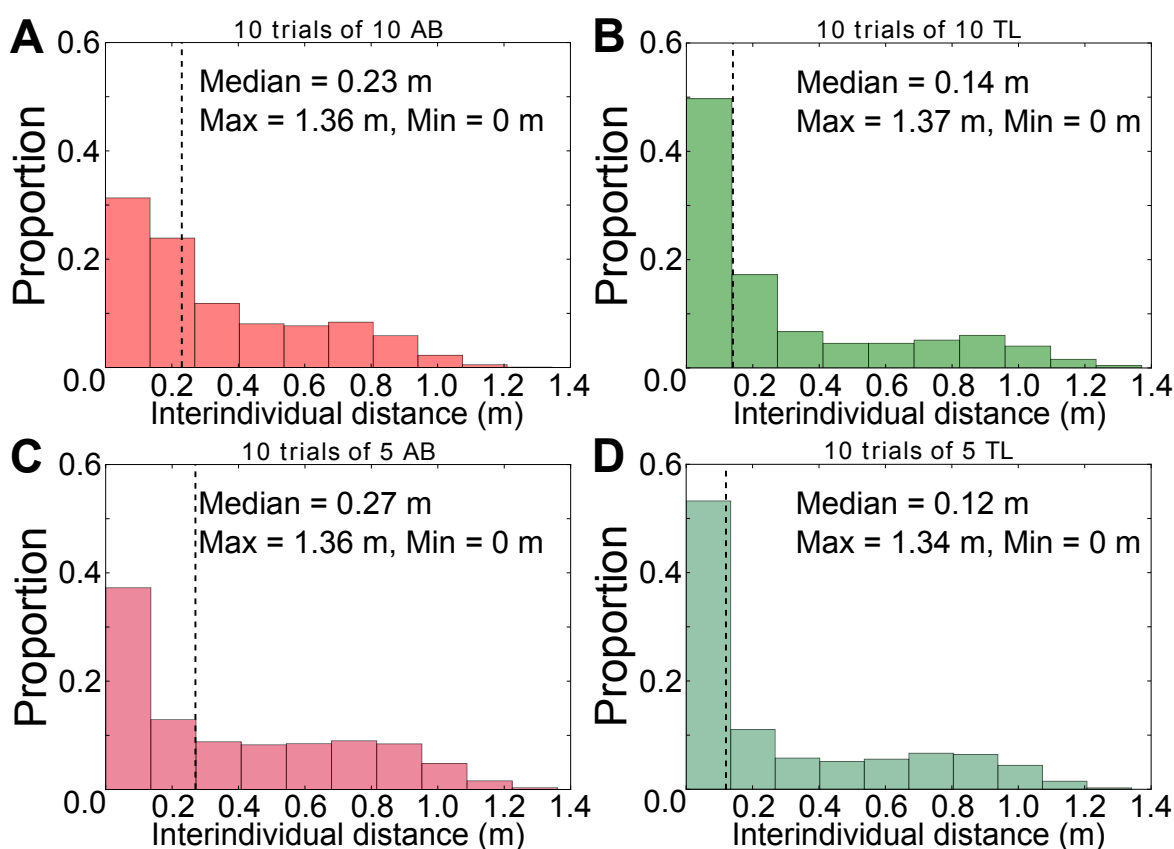


FIGURE 5.1 – **Interindividual distances for 10 trials in the square arena with two cylinders** with (A) 10 AB zebrafish ($N = 22\,480\,363$ distances), (B) 10 TL zebrafish ($N = 20\,981\,798$ distances), (C) 5 AB zebrafish ($N = 5\,169\,077$ distances) and (D) 5 TL zebrafish ($N = 4\,578\,036$ distances). Where N is the number of measured distances. The distributions show that groups of TL zebrafish have a stronger cohesion than groups of AB zebrafish. Although group size does not change this distribution in groups of TL strain, it has a strong impact on the AB strain. Distributions of the interindividual distances of 10 AB and 10 TL are different, 5 AB and 5 TL are different, 5 AB and 10 AB are different and 5 TL and 10 TL are different (see in the text the results of the statistical tests).

The distributions of the average interindividual distances measured at each time step confirm these results (Figure 5.2, Kolmogorov-Smirnov test, 5 AB vs 10 AB, $D = 0.433$, $p <$

0.001; 5 TL vs 10 TL, $D = 0.051$, $p < 0.001$; 10 AB vs 10 TL, $D = 0.333$, $p < 0.001$; 5 AB vs 5 TL, $D = 0.464$, $p < 0.001$). The medians of the distributions of the average interindividual distances for 10 AB is 0.33m, for 10 TL is 0.29m, for 5 AB is 0.39m and for 5 TL is 0.30m. Moreover, the time series of the average interindividual distance reveals that the cohesion of the fish decreases for both strains and both group sizes through the time (Figure ?? of the supplementary materials).

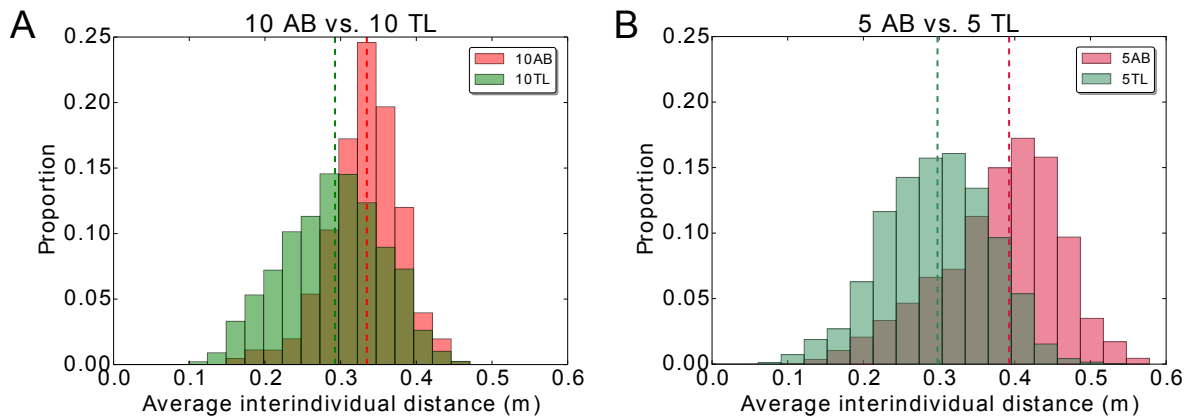


FIGURE 5.2 – **Average interindividual distance in the square arena with two cylinders** (A) for 10 AB zebrafish ($N = 518960$ measures) versus 10 TL zebrafish ($N = 500794$ measures). The red distribution represents 10 trials with groups of 10 AB zebrafish and the green represents 10 trials with groups of 10 TL zebrafish; (B) for 5 AB zebrafish ($N = 528357$ measures) versus 5 TL zebrafish ($N = 495659$ measures). The red distribution represents 10 trials with groups of 5 AB zebrafish and the green is for 10 trials with groups of 5 TL zebrafish. Dashed lines represent medians. TL zebrafish are more cohesive than AB zebrafish. Smaller groups of AB zebrafish show a shift to higher values. The distributions of the average interindividual distances of 10 AB and 10 TL are different, 5 AB and 5 TL are different, 5 AB and 10 AB are different and 5 TL and 10 TL are different.

In the presence of the floating disks, TL zebrafish were also significantly more cohesive than the AB zebrafish, as shown by the distribution of the interindividual distances (medians for 10 AB : 0.35m, for 10 TL : 0.23m, Figure 5.3, Kolmogorov-Smirnov test, $D = 0.135$ and $p < 0.001$). The previous analysis matches with the one obtained for the measures of average interindividual distances (medians for 10 AB : 0.45m, for 10 TL : 0.41m, Figure 5.4, Kolmogorov-Smirnov test, $D = 0.230$ and $p < 0.001$).

5.4.2 Group sizes affect strain preferences for landmarks

In the presence of the two cylinders, the groups of 10 AB zebrafish are mainly present along the wall of the tank and around the cylinders, as shown by their average probability of presence computed for the 10 replicates, each of one hour observation time (Figure 5.5). On the contrary, groups of 5 TL, 10 TL and 5 AB zebrafish are less observed near the cylinders but are still present along the walls of the tank (Figure 5.5). With the

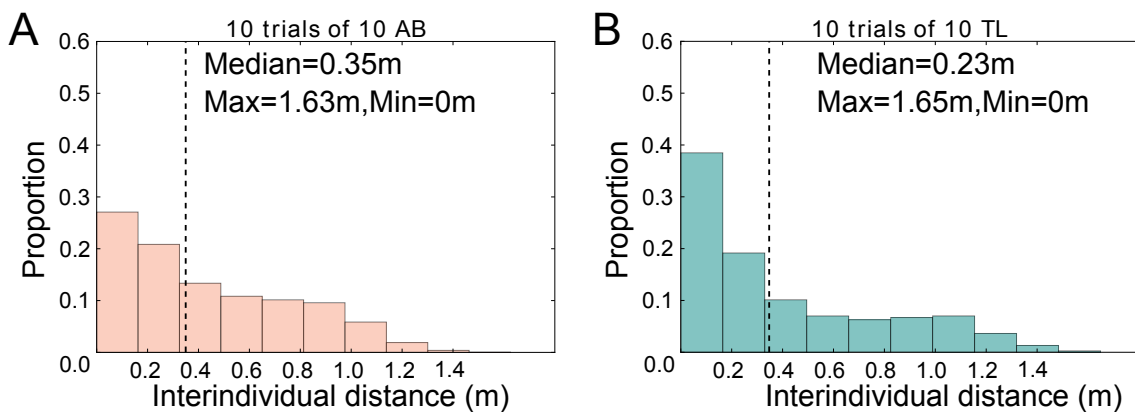


FIGURE 5.3 – **Interindividual distances for 10 trials in the square arena with two disks** with groups of (A) 10 AB zebrafish ($N = 1\,620\,450$ distances), (B) 10 TL zebrafish ($N = 1\,620\,450$ distances) in a tank with two disks. N is the number of measure of distance. Distribution of the interindividual distance shows that groups of TL zebrafish have a stronger cohesion than groups of AB zebrafish. Max and min show the maximum or minimum distances found between fish. A Kolmogorov-Smirnov test shows that the distributions of the interindividual distances of 10 AB and 10 TL are different.

two disks we observed similar behaviours than in the previous experiments with cylinders. The maximum probability of presence under the disks with AB zebrafish reaches 4.5×10^{-3} when for TL zebrafish it reaches only 1×10^{-3} (Figure 5.6). Again, TL zebrafish spent the majority of their time near the borders of the tank. The probabilities of presence computed for each experiment are shown in the supplementary materials (Figures 5.11, 5.12, 5.13, 5.14, 5.15, 5.16).

Then, we studied in more details the dynamics of the presence of groups of 10 zebrafish near the cylinders. The fish of the AB strain form a cohesive group that regularly transits from one landmark to the other one at the beginning of the trial. Then, the group starts to split in multiple subgroups and the periodicity of the visits becomes less regular (Figure 5.17). These oscillations are also observed for groups of the TL strain but contrarily to AB zebrafish, this phenomenon is observed for the whole experimental time (Figure 5.18). To quantify the dynamics of these transitions, we computed the number of majority events detected near one of the two landmarks or outside of them. A majority event was counted when 7 or more individuals were simultaneously present in the same zone independently of the duration of this majority event. Figure 5.7A shows that the median and mean number of majority events are always smaller with the TL strain, but this difference is only significant for the majorities detected near one of the cylinders (cylinder 1, Mann-Whitney U test, $U = 26$, $p = 0.038$; cylinder 2, Mann-Whitney U test, $U = 48$, $p = 0.455$; outside, Mann-Whitney U test, $U = 38$, $p = 0.192$). We also characterised the transitions of the fish from one landmark to the other one by analysing the succession of majority events. In particular, we counted the number of "Collective transitions" (*i.e.* two majority events

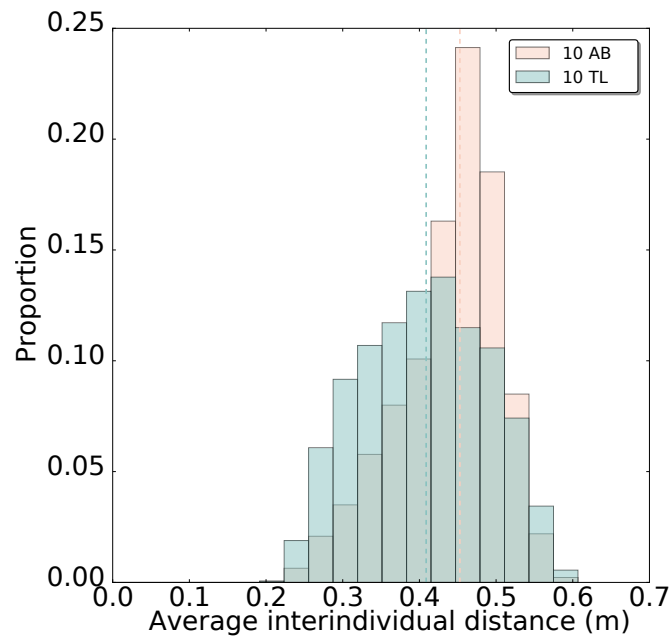


FIGURE 5.4 – **Average interindividual distance in the square arena with two disks** for 10 AB zebrafish ($N = 36010$ measures) versus 10 TL zebrafish ($N = 36010$ measures). The orange distribution represents 10 trials with groups of 10 AB zebrafish and the blue-green represents 10 trials with groups of 10 TL zebrafish. Dashed lines represent medians. TL zebrafish are more cohesive than AB zebrafish. The distributions of the average interindividual distances of 10 AB and 10 TL are different.

nearby different cylinders separated by a majority outside), the number of "One-by-one transitions" (*i.e.* succession of a majority event in one cylinder and a majority event in the other cylinder) and finally the number of "Collective U-turns" (*i.e.* two majority events in the same cylinder separated by a majority outside). It reveals that the main transitions occurring for AB zebrafish are the collective ones while some collective U-turns and almost no individual transitions were detected (Figure 5.7B red). Similarly, almost no individual transition was observed for the TL zebrafish that perform mainly collective transitions (Figure 5.7B green). TL zebrafish performed also numerous collective U-turns. The absence of individual transitions reveals that both strains are mostly swimming in groups but with different collective dynamics. We compared the results with Mann-Whitney U tests : "One-by-one transitions" ($U = 3.0$, $p < 0.001$) and "Collective U-turns" ($U = 27.5$, $p < 0.050$) between AB and TL are significantly different when "Collective transitions" between AB and TL are not ($U = 40$, $p = 0.236$).

To highlight the differential effects of the strains and the group sizes on space fidelity around cylinders, we measured the proportion of positions that were detected at 25 cm from the centre of the cylinders (Figure 5.8). This measure confirms that groups of 10 AB zebrafish were more present near the cylinders than groups of 5 AB. In contrast, while

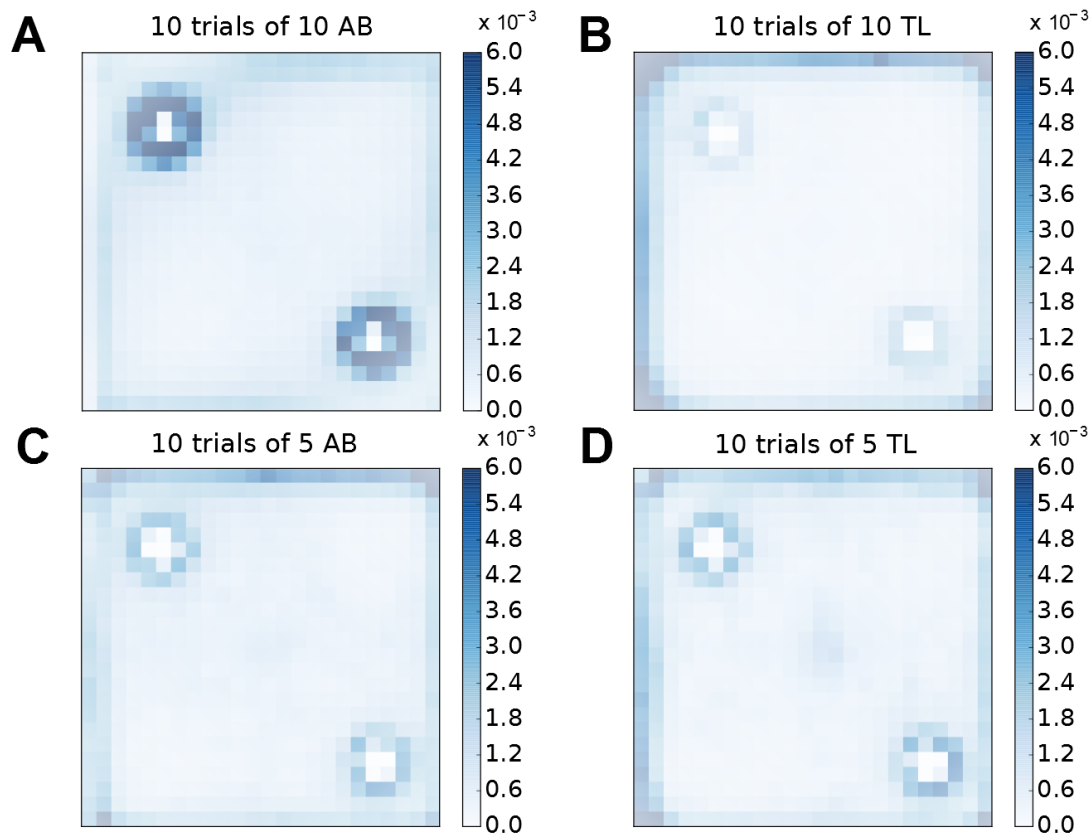


FIGURE 5.5 – **Probability of presence** of (A) 10 AB zebrafish, (B) 10 TL zebrafish, (C) 5 AB zebrafish and (D) 5 TL zebrafish in a tank with two cylinders. The probability is calculated on the positions of all zebrafish (i. e. 5 or 10 individuals) observed during one hour and cumulated for 10 trials. The response to the landmarks is strain and group size dependent : while 5 AB and 5 TL zebrafish show similar probability of presence near the cylinders, a larger group size of AB increases the response to the landmarks but decreases the response of groups of 10 TL.

groups of 5 TL responded similarly to groups of 5 AB, groups of 10 TL zebrafish were less detected near the cylinders. A two-way ANOVA (group size, strain, $n = 10$ for each experimental conditions) indicated a non-significant effect of the group size ($p = 0.07$, $F = 3.59$, $df = 1$) but a significant effect of the strain ($p < 0.001$, $F = 43.17$, $df = 1$) and a significant interaction strain/group size ($p < 0.001$, $F = 35.38$, $df = 1$) on the attractivity of the cylinders. The interaction effect indicates here a strain-specific effect of the group size on the time spent near the landmarks : groups of 10 AB are more attracted by the cylinders than groups of 5 AB but on the contrary, 10 TL are less detected near the cylinders than groups of 5 TL. To confirm this observation, we compared the proportions for all groups (5 or 10 zebrafish, AB or TL strain) with a one-way ANOVA. The test confirmed that the size of the group and the type of strain have a significant influence on the attractivity of the cylinders ($p < 0.001$, $F = 27.38$, $df = 3$). Finally, a Tukey's honest significant difference criterion post-hoc test shows that attractivity of the cylinders is always different except for the couple 5 AB versus 5 TL. This serie of tests confirmed that groups of 10 AB are more attracted by the

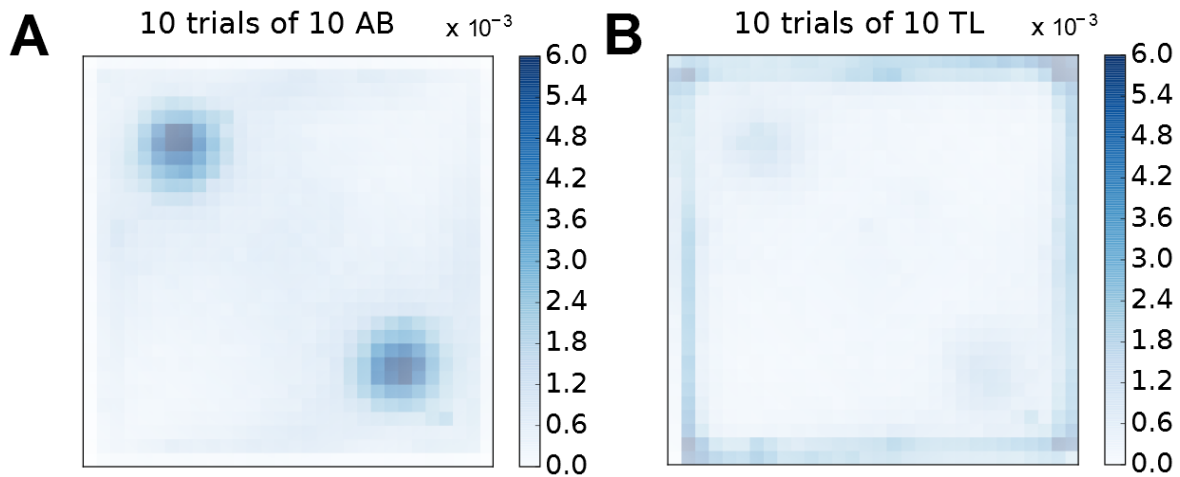


FIGURE 5.6 – **Probability of presence** of (A) 10 AB zebrafish in a tank with two disks, (B) 10 TL zebrafish in a tank with two disks. The probability is calculated on the positions of all zebrafish observed during one hour and cumulated for 10 trials. Attractivity to landmarks is strain dependent : the probability of presence of finding 10 AB zebrafish around the landmarks is 2 times higher than that of 10 TL zebrafish.

cylinders than groups of 5 AB and 5 TL which are more attracted by cylinders than groups of 10 TL.

Finally, we compared the probability to be near the landmarks (cylinders or disks) for 10 AB and 10 TL zebrafish with a two-way ANOVA (Figure 5.9). It revealed that the type of landmarks ($p < 0.001$, $F = 11.37$, $df = 1$) and the strain of zebrafish affect the attraction ($p < 0.001$, $F = 102.95$, $df = 1$) while there is also an evidence of an interaction effect between type of landmarks and strains ($p = 0.02$, $F = 5.67$, $df = 1$). To confirm this observation, we compared the proportions for all groups (10 zebrafish, AB or TL strain in presence of cylinders or disks) with a one-way ANOVA. The test confirmed that the type of the strain and the type of the landmark have a significant influence on the attractivity of the cylinders ($p < 0.001$, $F = 39.99$, $df = 3$). Finally, a Tukey's honest significant difference criterion post-hoc test shows that all paired comparisons are significantly different except for the 10 AB disks and 10 AB cylinders. This serie of tests confirmed that groups of 10 AB zebrafish are more attracted by the landmarks than groups of 10 TL which show more attraction for cylinder type than disk type.

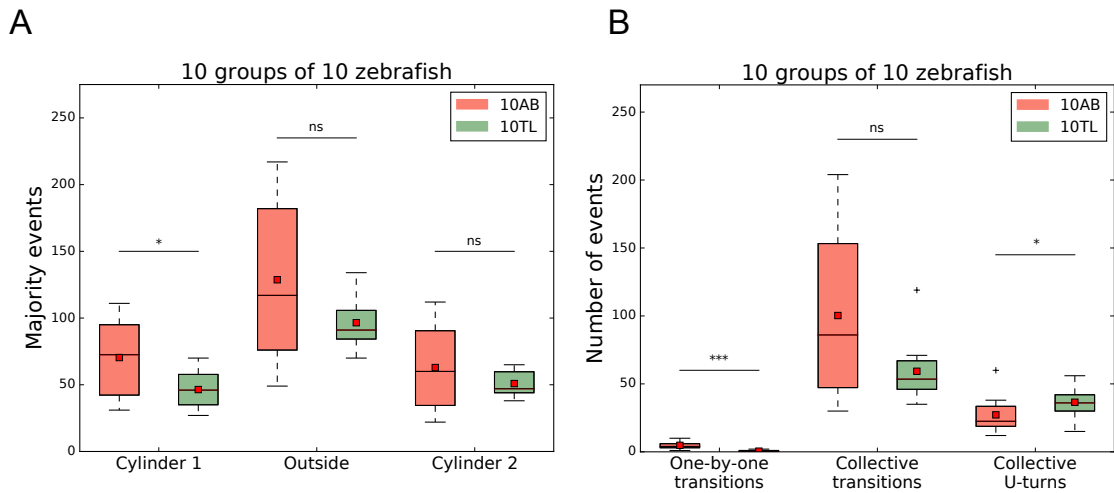


FIGURE 5.7 – **Landmark occupancy and transitions** for 10 trials of 10 AB zebrafish and 10 TL zebrafish. (A) Number of majority events occurring around the cylinders and outside. A majority event was considered as soon as more than or equal to 7 fish are aggregated in the same zone. (B) Number of transitions of the majority from one zone to another one. We mainly looked at "One by one" transitions (the fish transit one by one from one cylinder to the other), *Collective transitions* (the whole group transits between both cylinders through the outside area) and *Collective U-turns transitions* (the group go back to the previous cylinder). For both strain, while several U-turns were observed, the majority of transitions were made in groups (Collective transitions) and only a few were made one-by-one. The TL strain significantly differs from the AB strain by performing significantly less One-by-one transitions and more Collective U-turns. Each boxplot is composed of 10 values of majority events or numbers of events. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non significant.

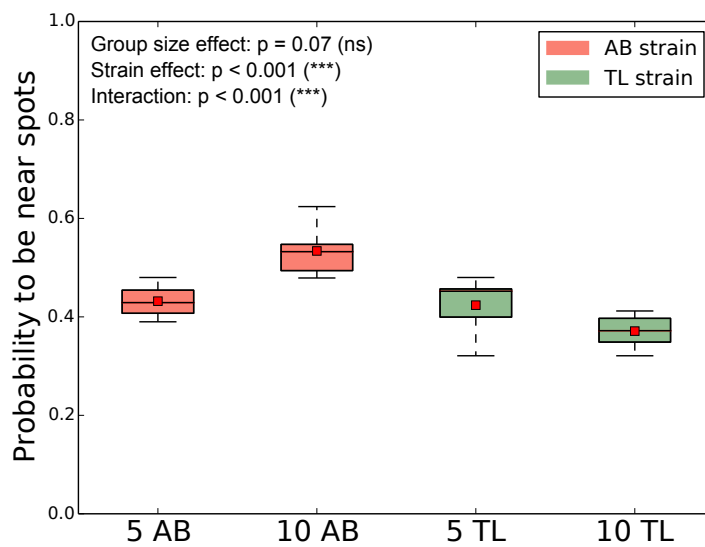


FIGURE 5.8 – **Probability to be at 25 cm from the center of the cylinders** for 10 trials with 5 AB, 10 AB, 5 TL or 10 TL zebrafish in a 1m² tank with two cylinders. The black line shows the median, the red square shows the mean. Statistical tests show that groups of 10 AB are more attracted by the cylinders than groups of 5 AB and 5 TL which are more attracted by cylinders than groups of 10 TL. $N = 10$ measures for 5 AB, 10 AB, 5 TL and 10 TL. Each boxplot is composed of 10 values of probability. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non significant.

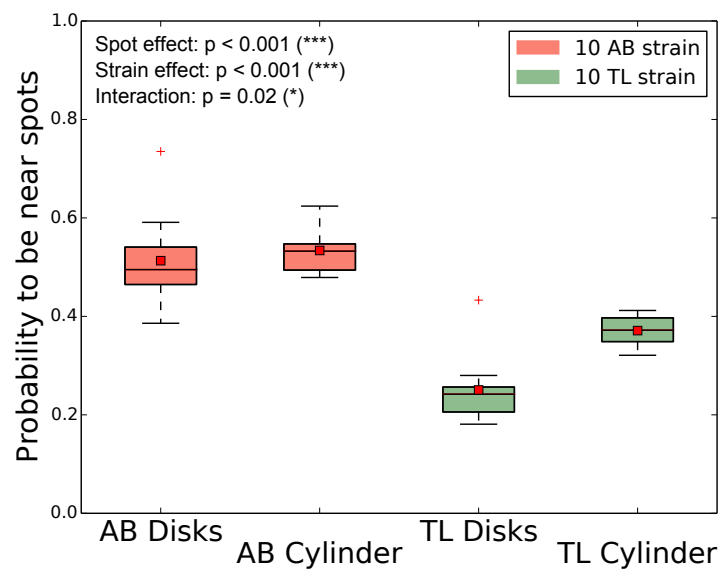


FIGURE 5.9 – **Probability to be at 25 cm from the center of cylinders or disks** for 10 trials. Groups of 10 AB or 10 TL zebrafish in a tank with two cylinders or two disks. The black line shows the median, the red square shows the mean. A serie of tests shows that groups of 10 AB are attracted by cylinders as much as disks, groups of 10 TL are more attracted by cylinders than disks, groups of 10 AB are more attracted by the cylinders and the disks than groups of 10 TL. N = 10 measures for AB disk, AB cylinder, TL disk and TL cylinder. Each boxplot is composed of 10 values of probability
 * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non significant.

5.5 Discussion

We investigated whether collective motion and collective choice can differ in groups of 5 and 10 individuals of the same species (zebrafish *Danio rerio*) but of different strains (AB versus TL) in the presence of two identical landmarks. One hour observation trials show that the zebrafish groups do not select one of the two landmarks. The fish were mainly swimming together and oscillating from one landmark to the other with short resting times. Thus, while all individuals can be present at the same landmark during few seconds (Figure 5.17 and Figure 5.18 of the supplementary materials), the probability of presence computed for the entire experimental time shows that the fish were equally present at both stimuli. Therefore, no collective choice emerged on the long duration for both strains of zebrafish and group sizes. Hence, long or short study durations can reveal opposite conclusions on collective motions. In other species, site fidelity has been studied for longer time period. It has been evidenced that *Hemigrapsus sanguineus* exhibited low site fidelity after 24 hours : 17.8% and 2.3% of the released crabs were recovered within 0.1 m from the two studied sites [Brousseau et collab. \[2002\]](#); for *Helograpsus haswellianus*, the authors have shown that the recapture rates of marked crabs were very low across their 4 week lunar study (5.8% and 5.3% on two different sites at a distance of 70 kilometers), while recaptures often occurred in the same trap (31.3% and 25%) [Katrak et Dittmann \[2011\]](#). The authors suggest that this low rate of site fidelity could be due to foraging issues. For *Genyonemus lineatus*, researchers report evidences of site fidelity during the 7 first days of their study (over 240 days) with low and variable residency times [Wolfe et Lowe \[2015\]](#). For *Cynoscion regalis*, it has been found that there is a strong link between the birth location of the parents and their spawning location : from 60 to 81% [Thorrold et collab. \[2001\]](#).

Our methodology is complementary to typical Y-maze experiments. We extend and compare their conclusions to our observations with repeated interactions between the fish and their environment. During an hour, the collective behaviour of zebrafish contrasts with other collective species in which spatial fidelity emerges from the interactions between the individuals that take place in the resting sites (in cockroaches [Ame et collab. \[2004\]](#), in hymenoptera [Franks et collab. \[2002\]](#)). These oscillations from one site to the other one could originate from individual differences among group members : *bold* and *shy* behavioural profiles have been evidenced in zebrafish according to the intrinsic propensity of each fish to explore new environments [Dahlbom et collab. \[2011\]](#); [Guayasamin \[2013\]](#). It has been shown that zebrafish with high boldness lost their shoal cohesion when making decisions unlike other species (*Gasterosteus aculeatus*) where boldness as attractor has been identified [Harcourt et collab. \[2009\]](#). In this context, the presence of bolder fish in the group could favour the transition from one spot to the other one while groups

composed only by shy individuals could show less frequent departures [Leblond et Reeb](#) [2006]. Boldness and shyness as modifiers of group behaviour occur also in mammals, for example, where bold sheep tend to split big groups in smaller subgroups of equal size [Michelena et collab.](#) [2009]. We did not identify significant differences between both strains for collective transitions but we revealed significant differences for the "one-by-one" transitions and the collective U-turns. AB zebrafish show more "one-by-one" transitions than TL and TL zebrafish show more collective U-turns than AB. We could categorize the "one-by-one" transitions as more dangerous because they occur when the group transit from a landmark to the other one, one fish after another. The fish are thus exposed in the tank and we could link these transitions with bold personalities. Following the same reasoning collective U-turns can be assimilated as shy events because fish go back in their previous known location. Hence, there could be a difference of boldness between both strains that might be highlighted by a deeper analysis of the transitions.

A more detailed analysis shows quantitative differences among the two studied strains and group sizes. Concerning the response of the fish to the landmarks, we highlight that groups of 5 AB and TL zebrafish show the same attraction for the cylinders by computing the probability for the fish to be observed near these landmarks. This attraction increases for groups of 10 AB zebrafish but decreases for groups of 10 TL zebrafish. This strain difference is also observed in the experiments with floating disks. In addition, the type of the landmarks seems to be determinant for TL zebrafish as they prefer objects immersed in the water column than objects lying on the surface of the water. Hence, differences of collective behaviour between the two tested strains of zebrafish exists.

These different responses to heterogeneities may be based on the intrinsic preference of the fish of a particular strain for congeners or for landmarks. Such difference has already been shown in shoaling tendency between several strains of guppies [SEGHERS et collab.](#) [1995] and zebrafish [Wright et collab.](#) [2003], [Wright et collab.](#) [2006]. In their natural environment, fish have to balance the costs of risks and benefits of moving in groups or staying near landmarks [Millot et collab.](#) [2009]. Our results suggest that there are more collective transitions than collective U-turns and "one-by-one" transitions. It means that zebrafish (whatever the strain) prefer to transit in group and thus avoid group fission when crossing an open area. Moving in groups first of all prevents the fish to be static preys, and second allow spatial recognition and easier food and predators detection. The drawback is that the takeover of the fish on the territory is punctual and they have less chance to find areas where they can hide. Staying around landmarks gives the fish a feeling of control of the territory and the possibility to hide from predators. In that case the drawback is that the preys will rarely cross the territory of the fish.

Regarding the structure of the group, we notice that whatever the group size of TL zebrafish, the cohesion of the group does not change and is always stronger than those

of groups of AB zebrafish. Also, the bigger the group of AB zebrafish, the stronger the cohesion. These differences of group cohesion may be based on differences of physical features between AB and TL zebrafish. Cohesion differences could be explained by phenotype differences between the two strains. Some studies demonstrated that a large variability exists in the individual motion and shoaling tendency of the zebrafish according to their age or strain. For example, adults AB and casper zebrafish swim longer distance than ABstrg, EK, TU or WIK zebrafish [Lange et collab. \[2013\]](#). Likewise, the interindividual distance between shoal members decreases from 16 body length to 3.5 body length between day 7 and 5 months after fertilization [Buske et Gerlai \[2011\]](#). Also, it has been demonstrated that the fin size has an impact on the swimming performance and the behaviour of the zebrafish [Plaut \[2000\]](#). AB and TL zebrafish show different fin lengths and different patterns on the skin : TL zebrafish are homozygous for leo^{t1} and lof^{dt2} , where leo^{t1} is a recessive mutation causing spotting in adult zebrafish and lof^{dt2} is a dominant homozygous viable mutation causing long fins [Iovine et Johnson \[2000\]](#), [Watanabe et collab. \[2006\]](#). Thus, AB zebrafish have short fins and TL zebrafish show long fins. One may suggest that TL zebrafish move a higher quantity of water with their long fins when swimming and thus emit a stronger signal of presence (hydrodynamical signal). Thus, it may be easier for conspecifics in the moving shoal to perceive the signal through their lateral line and realign themselves according to their conspecifics. If the realignment becomes easier, it is simpler for TL zebrafish to keep their position in the shoal, which increases its cohesion. Following a similar hypothesis, the signal of presence is weaker for AB zebrafish due to their shorter fins. Thus, realignment in the moving shoal is less performant and their cohesion decreases. [Hemmings \[1966\]](#) and [Partridge et Pitcher \[1980\]](#) showed that fish use vision for attraction and the lateral line for repulsion. Recently, it has been revealed that the visual field (binocular and lateral) modify the group cohesion [Pita et collab. \[2015\]](#). The zebrafish strain showing the bigger visual field should be less cohesive. However, none of the previous mutations (leo and lof) could explain these differences of visual fields in both strains of zebrafish. The lateral line could also explain the differences of cohesion between AB and TL zebrafish : the mutation of the leo gene (TL zebrafish) may have an effect on it, lowering its performances. Hence, unlike the AB zebrafish, the repulsion may occur when TL zebrafish are closer to each other, forcing them to be more cohesive. Each of these hypotheses could explain the collective behaviours observed during the experiments and nothing prevents merging all of them.

Finally, we did not quantified aggressive behaviour during the experiments. There are several studies trying to find a link between aggression and shoal size. In [Morgan \[1988\]](#) the authors show that aggressive interactions of *Pimephales notatus* decrease significantly as shoal size increases when [Rehnberg et Smith \[1988\]](#) shows that there is no clear evidence between levels of aggression and shoal size with *Danio rerio*. The issue of ag-

gressive behaviours could be left open for another study.

In conclusion, this study demonstrates that behavioural differences exist at the individual and collective levels in the same species of animal. The analysis of the dynamics reveals that AB and TL zebrafish mainly oscillate in groups between landmarks. In addition, increasing the size of the group leads to opposite results for the two strains : groups of 10 AB zebrafish are proportionally more detected near the landmarks than groups of 5 AB while groups of 10 TL zebrafish are less attracted by the landmarks than groups of 5 TL. Finally, the two tested zebrafish strains show differences at the structural level : (1) groups of TL zebrafish are more cohesive than groups of AB zebrafish and (2) AB zebrafish collective responses to landmarks show that they are generally more present near the cylinders and floating disks than TL zebrafish. Thus, this study provides evidences that zebrafish do not select resting site on the midterm and highlights behavioural differences at the individual and collective levels among the two tested strains of zebrafish. Future studies of collective behaviour should consider the tested strains, the intra-strain composition of the shoals and the duration of each trial.

5.6 Methods

Fish and housing

We acquired 500 adult common laboratory wild-type zebrafish (200 AB strain and 300 TL strain) from Institut Curie (Paris) and raised them under the same conditions in tanks of 60L by groups of 50. The zebrafish AB line show a zebra skin, short tail and fin. The zebrafish TL line show a spotted skin, long tail and fin and barbel. Both strains are 3.5 cm long. The zebrafish used for the experiments are adult fish between 5 months and 18 months of age. During this period, zebrafish show a shoaling tendency allowing study of their collective behaviours. We kept fish under laboratory condition, 27°C, 500µS salinity with a 9 :15 day :night light cycle. The fish were fed two times per day (Special Diets Services SDS-400 Scientific Fish Food). Water pH is maintained at 7.5 and nitrites (NO²⁻) are below 0.3 mg/l. We measured the size of the caudal fins of 10 AB (about 0.4 cm) and 10 TL (about 1.1 cm) zebrafish.

Experimental setup

The experimental tank consists in a 1.2 m x 1.2 m tank confined in a 2 m x 2 m x 2.35 m experimental area surrounded by a white sheet, in order to isolate the experiments and homogenise luminosity. The wall of the experimental tank were covered with white tape and the water column is 6 cm. Water pH is maintained at 7.5 and Nitrites (NO²⁻) are below 0.3 mg/l. The experiments with disks were performed in the experimental tank while

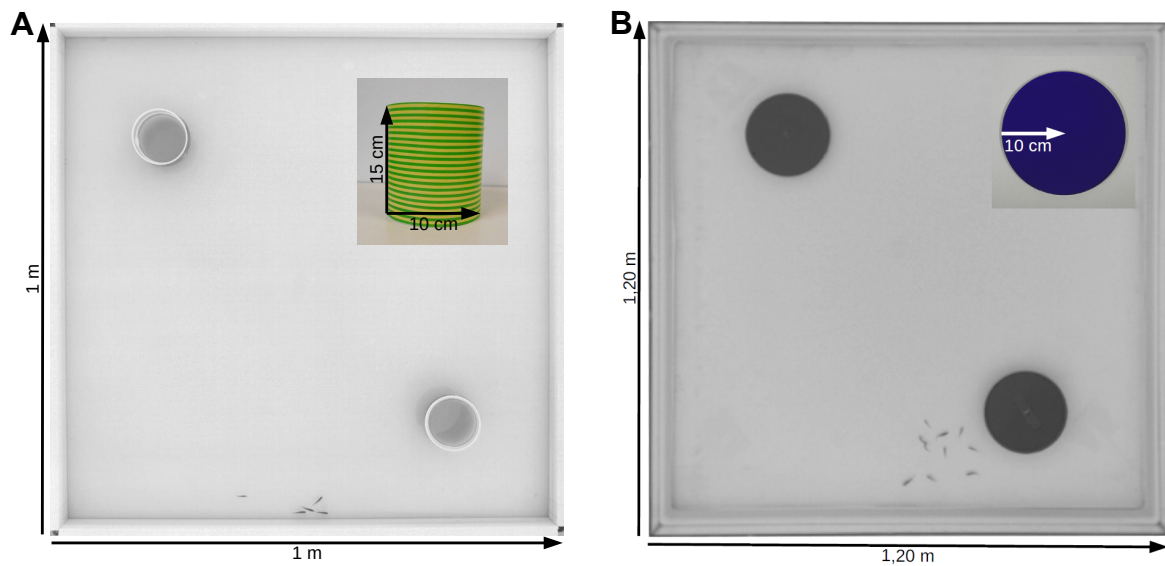


FIGURE 5.10 – (A) **Experimental setup** (1 m x 1 m) with two cylinders symmetrically placed and a magnified cylinder ($\phi = 10$ cm, Height = 15 cm). (B) **Experimental setup** (1.2 m x 1.2 m) with two blue perspex disks symmetrically placed and a disk ($\phi = 20$ cm). In the experimental tank, the water column is 6 cm. Luminosity is ensured by 4 fluorescents lamps of 80W placed on each side of the tank, on the floor and directed towards the walls to provide indirect lightning. The whole set-up is confined in a 2 m x 2 m x 2.35 m experimental chamber (cage) surrounded by white sheets to isolate the experiments and to homogenise luminosity.

those with cylinders were performed in a white square arena (1 m x 1 m x 0.15 m) placed in the experimental tank. Groups of zebrafish were randomly formed at the beginning of the experiments.

The experiments were recorded by a high resolution camera (2048 x 2048 px, Basler Scout acA2040-25gm) placed above the experimental tank and recording at 15 fps (frame per second). Luminosity is ensured by 4 fluorescents lamps of 80W placed on each side of the tank, on the floor and directed towards the walls to provide indirect lightning.

To trigger interest of fish, we placed symmetrically in the set-up either two floating disks ($\phi = 20$ cm) or two cylinders ($\phi = 10$ cm, Height = 15 cm) surrounded by yellow and green striped tape Gerlai [2014]; Lau et collab. [2011]; Saverino et Gerlai [2008]. To avoid the presence of a blind zone, the cylinders were slightly tilted toward the centre of the tank. The center of both disks and cylinders are at $25\sqrt{2}$ cm from two opposite corners along the diagonal of the tank (Figure 9.1).

Experimental procedure

We recorded the behaviour of zebrafish swimming in the experimental tank during one hour. Before the trials, the attractive landmarks are put in the setup and fish are placed with a hand net in a cylindrical arena (20 cm diameter) made of Plexiglas placed in the

centre of our tank. Following a five minutes acclimatisation period, this arena is removed and the fish are able to freely swim in the experimental arena. We performed 10 trials for each strain with the floating disks and 10 trials for each combination of parameters (number of fish x strain) with the cylinders for a total of 60 experiments. Each fish was never tested twice in the same experimental condition.

Tracking and Data analysis

The methodology based on massive data gathering [Reiser \[2009\]](#) has now become standard in studies on animal collective behaviour with flies, *Drosophila melanogaster* [Branson et collab. \[2009\]](#); [Dankert et collab. \[2009\]](#), birds, *Sturnus vulgaris* [Ballerini et collab. \[2008\]](#); [Miller et Gerlai \[2007, 2011\]](#) and fish, *Notemigonus crysoleucas* [Strandburg-Peshkin et collab. \[2013\]](#). The experiments with cylinders were recorded at 15 fps and tracked online by a custom made tracking system based on blob detection. We call a batch a group of 10 experiments. For these batches, each experiment consists of 540000 positions (10 zebrafish x 54000 frames) and 270000 positions (5 zebrafish x 54000 frames). For experiments with disks, we faced tracking troubles. Since the fish below the floating disks were difficult to distinguish by the program due to a lack of sufficient contrast, experiments with floating disk were tracked offline by two custom Matlab scripts. A first script automatically identifies the positions of the fish swimming outside of the floating disks by blob detection. Since this method did not allow a perfect detection of all the individuals, we developed a second script that was run after the first one and that plotted the frame where a fish (or more) was undetected for the user to manually identify the missing individual(s). It allowed us to identify the fish that were partially hidden during a collision/superposition with another fish or the fish that were situated under the floating disks. Since this analysis tool is time-costly, we only analysed 1 fps for all experiments with disks. For these batches, each experiment consists of 36000 positions (10 zebrafish x 3600 positions).

Since our tracking system did not solve collision with accuracy, we did not calculate individual measures but characterised the aggregation level of the group. The probability of presence of the fish was calculated by the cumulated positions of all individuals along the entire experiment. We also calculated the distance between each individual fish and the attractive landmarks (and averaged it) as well as the inter-individual distances between the fish and the average inter-individual distance. Finally, we computed the time of shelter occupancy as the time that is spent by the fish at less than 25cm of the attractive landmarks. These time sequences were calculated according to the number of fish present near the landmarks. All scripts were coded in Python using scientific and statistic libraries (numpy, pylab, scilab and matplotlib).

To compute the number of majority events, the number of fish was average over the

15 frames of every second. This operation guarantees that a majority event is ended by the departure of a fish and not by an error of detection during one frame by the tracking system. Figures 5.20 and 5.20 of the supplementary materials show the proportions of the durations of the the majority events before and after this interpolation.

Statistics

For the Figures 5.8 and 5.9, 10 measures of means of the probability for different groups of zebrafish to be near the landmarks are plotted. They have been tested using a two-way ANOVA. We then compared the data between each group using a one-way ANOVA and finally used a Tukey's honest significant difference criterion post-hoc test. We did these tests on MATLAB and chose 0.001 as significance level. In the Table 1 in the supplementary materials, we show the number of majority events after interpolation of the data at 1 fps. This table is related to the Figure 5.7. We used Mann-Whitney U tests to compare the number of events between strains, areas and transition types. These tests are performed on 10 values of majority events for each strain, area and transition type. These tests were made with the python package scipy. We chose 0.001 (***), 0.01 (**) and 0.05(*) as significance levels. For the Figure 5.1 as well as the Figures 5.2 and 5.3, we compared the distribution with Kolmogorov-Smirnov tests. These tests were made with the python package scipy. We chose 0.001 as significance level.

5.7 Annexe

Supplementary figures of "Strains differences in the collective behaviour of zebrafish (*Danio rerio*) in heterogeneous environment".

Experiments	Mean of percentages of tracking efficiencies
10 AB cylinders	96.05%
10 TL cylinders	92.73%
5 AB cylinders	97.80%
5 TL cylinders	91.77%
10 AB disks	100%
10 TL disks	100%

TABLEAU 5.1 – Means of percentages of tracking efficiencies.

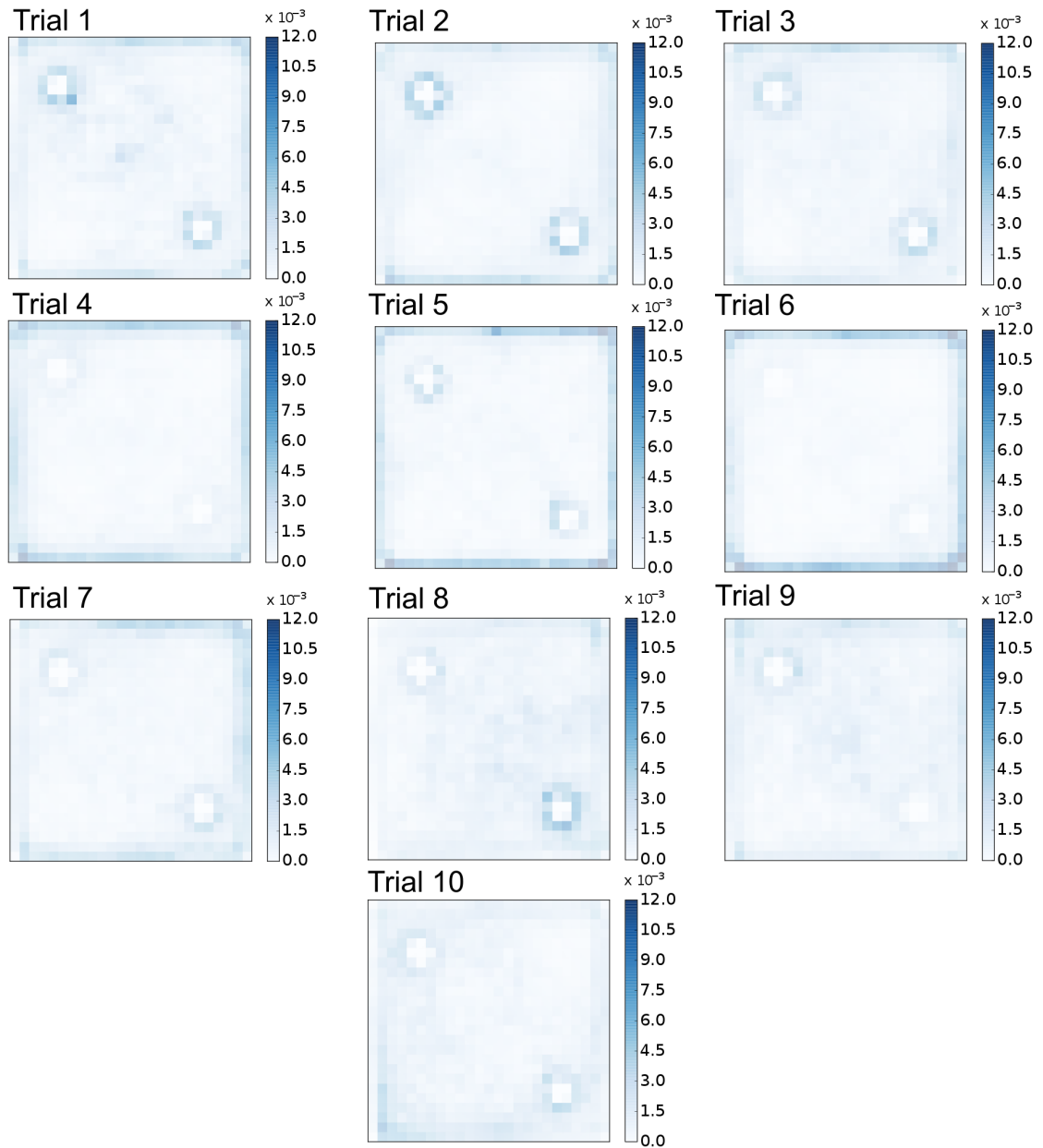


FIGURE 5.11 – **Probabilities of presence** of 10 trials of 5 AB zebrafish with two cylinders. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

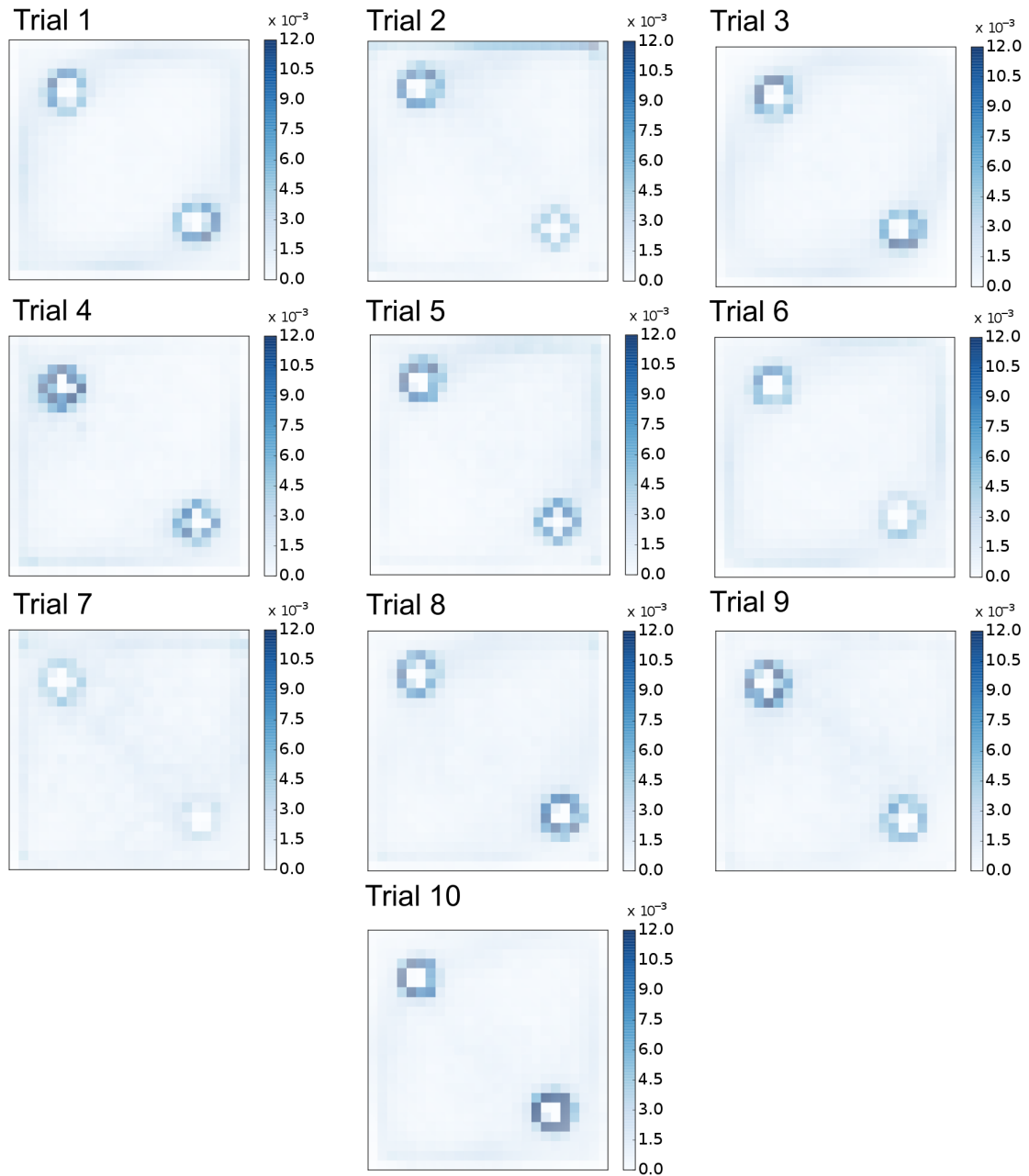


FIGURE 5.12 – **Probabilities of presence** of 10 trials of 10 AB zebrafish with two cylinders. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

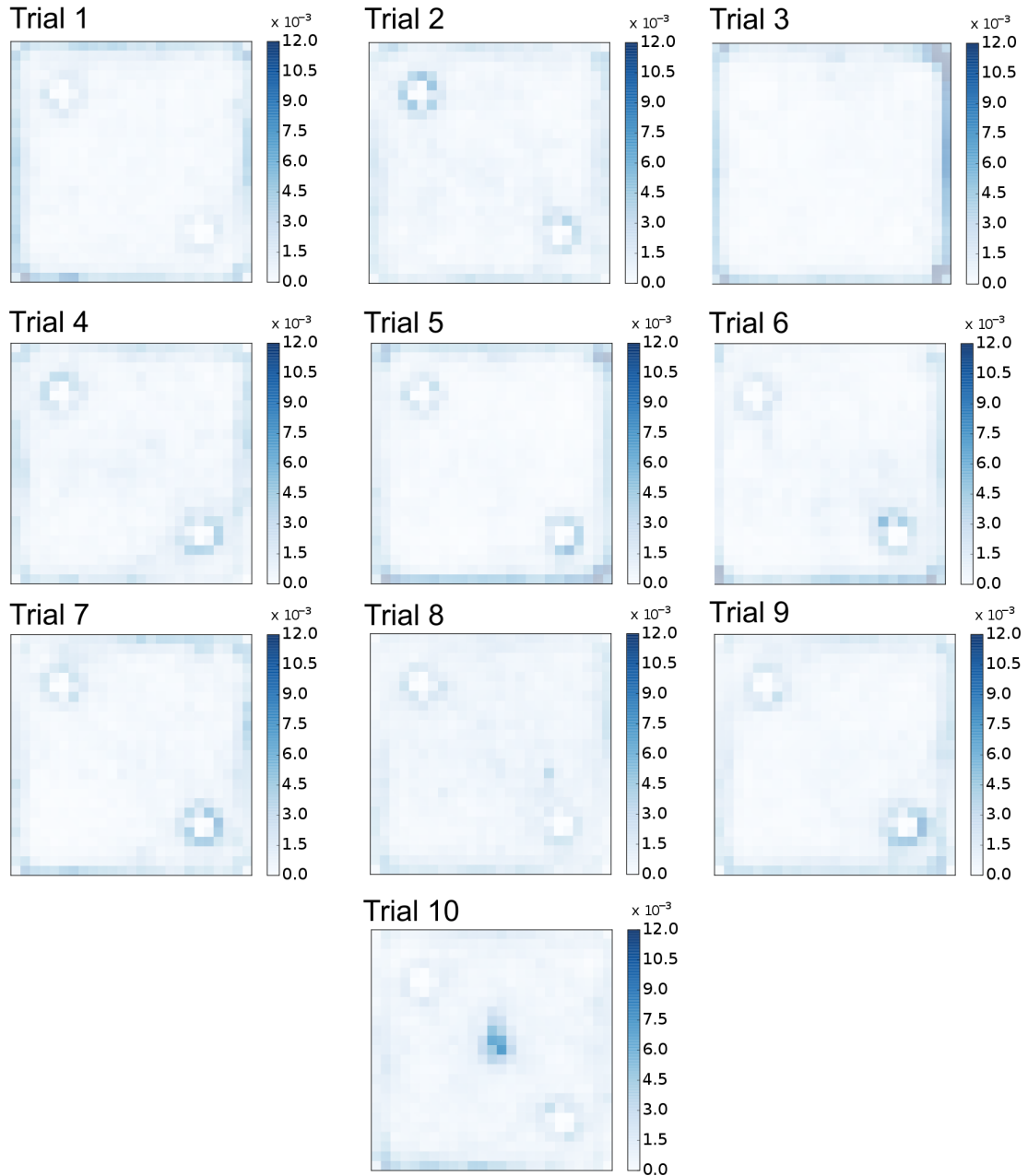


FIGURE 5.13 – **Probabilities of presence** of 10 trials of 5 TL zebrafish with two cylinders. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

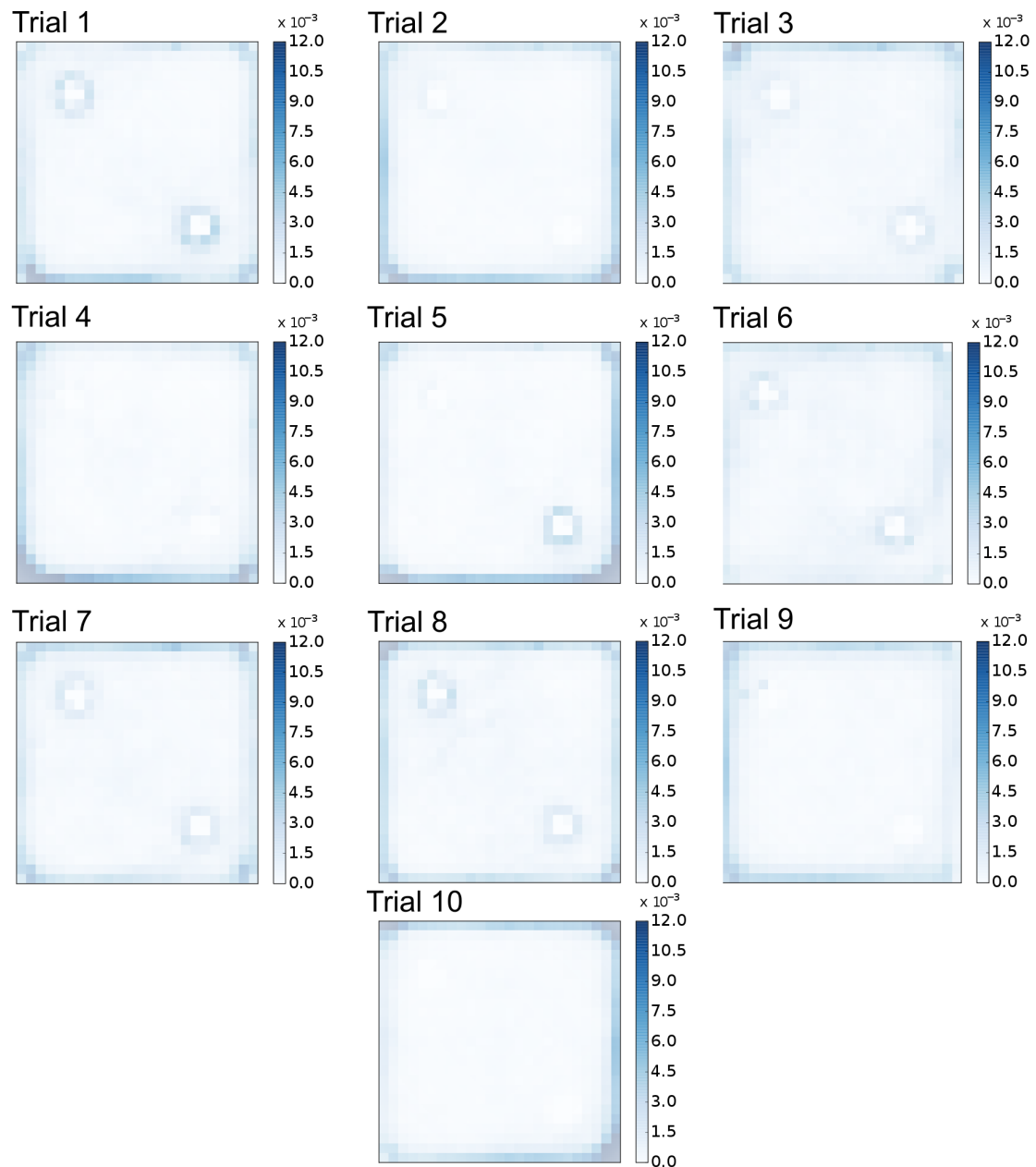


FIGURE 5.14 – **Probabilities of presence** of 10 trials of 10 TL zebrafish with two cylinders. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

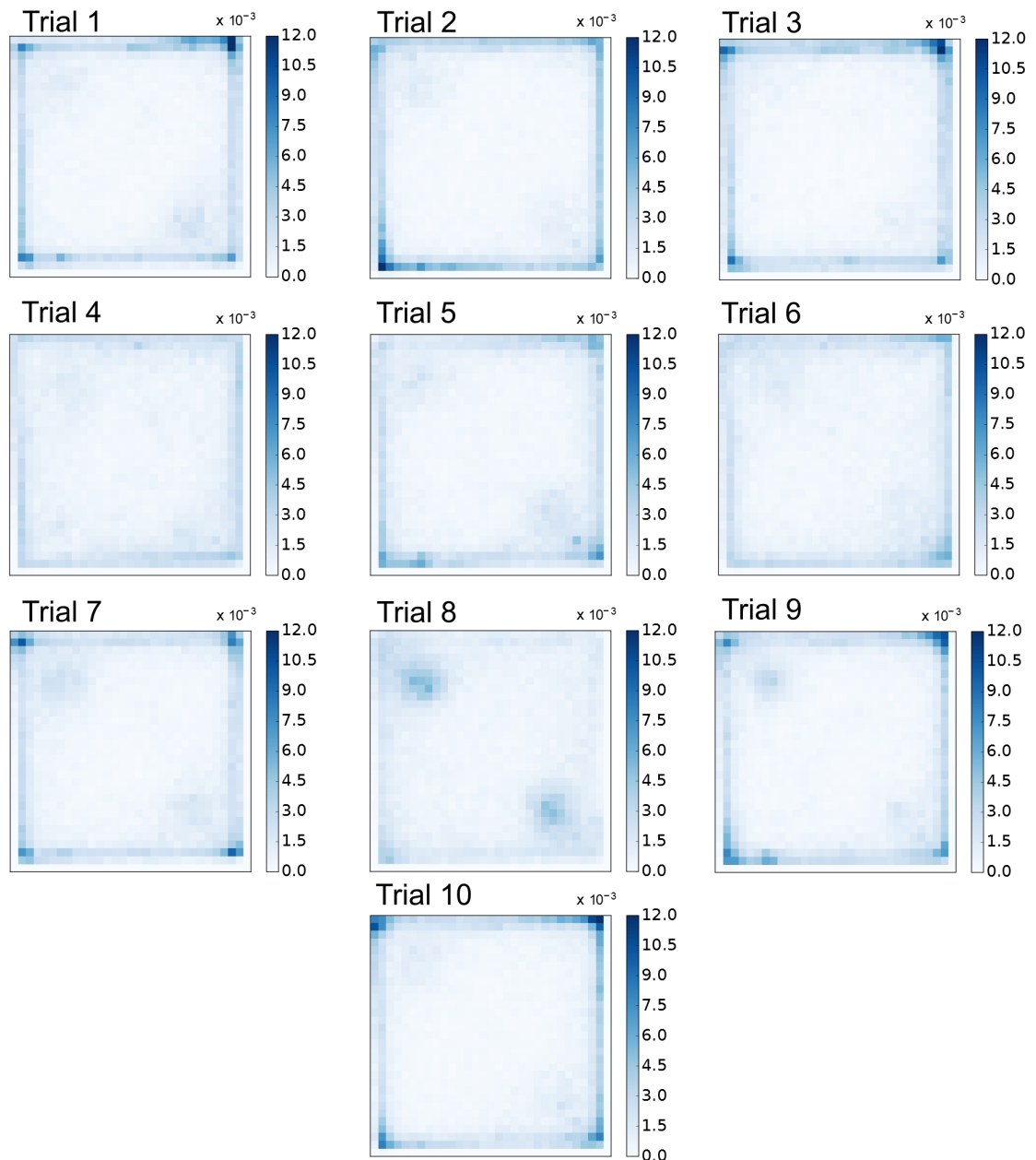


FIGURE 5.15 – **Probabilities of presence** of 10 trials of 10 TL zebrafish with two disks. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

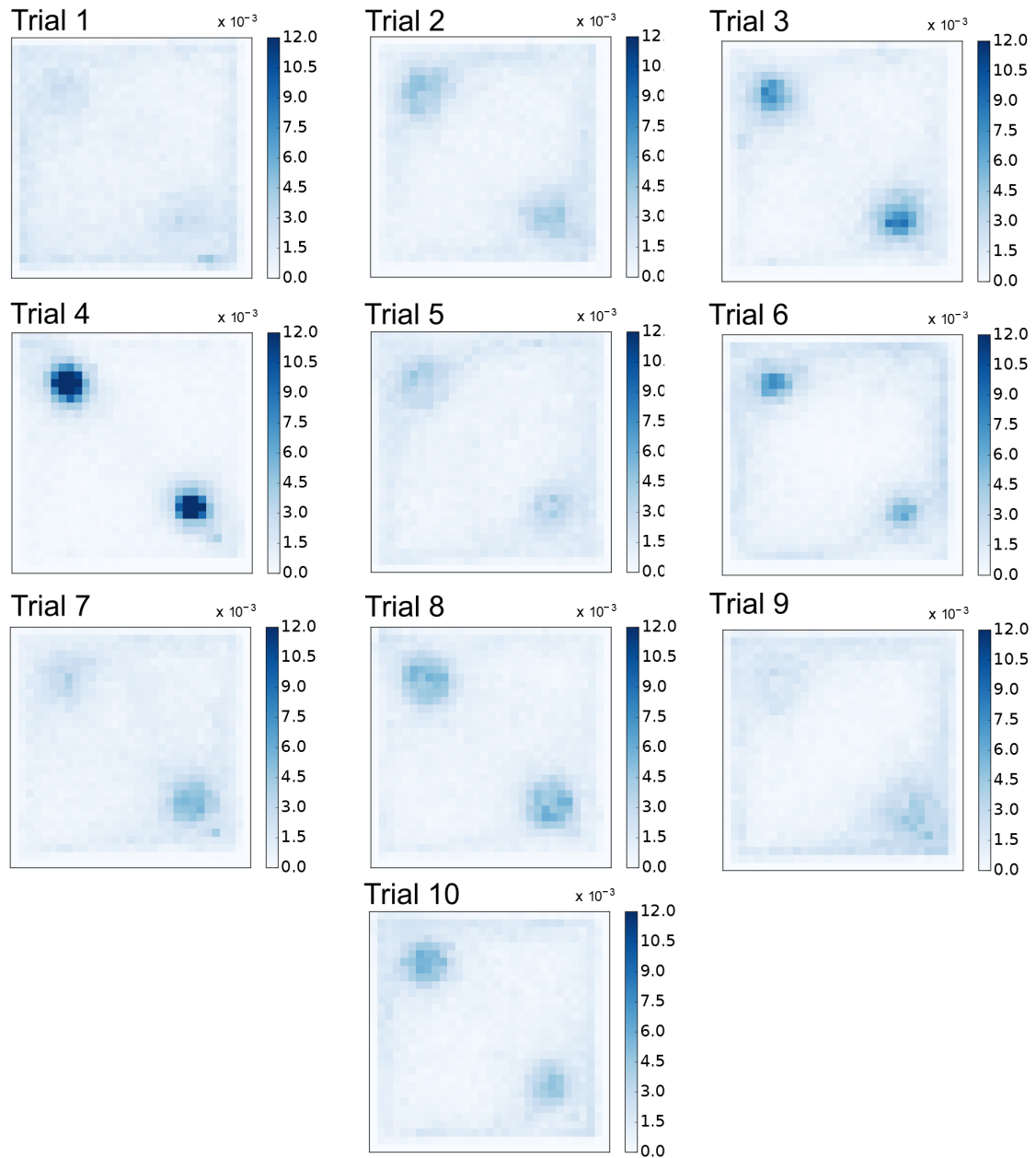


FIGURE 5.16 – **Probabilities of presence** of 10 trials of 10 AB zebrafish with two disks. The probability is calculated on the positions of all zebrafish observed during one hour. The bluer the more fish detected.

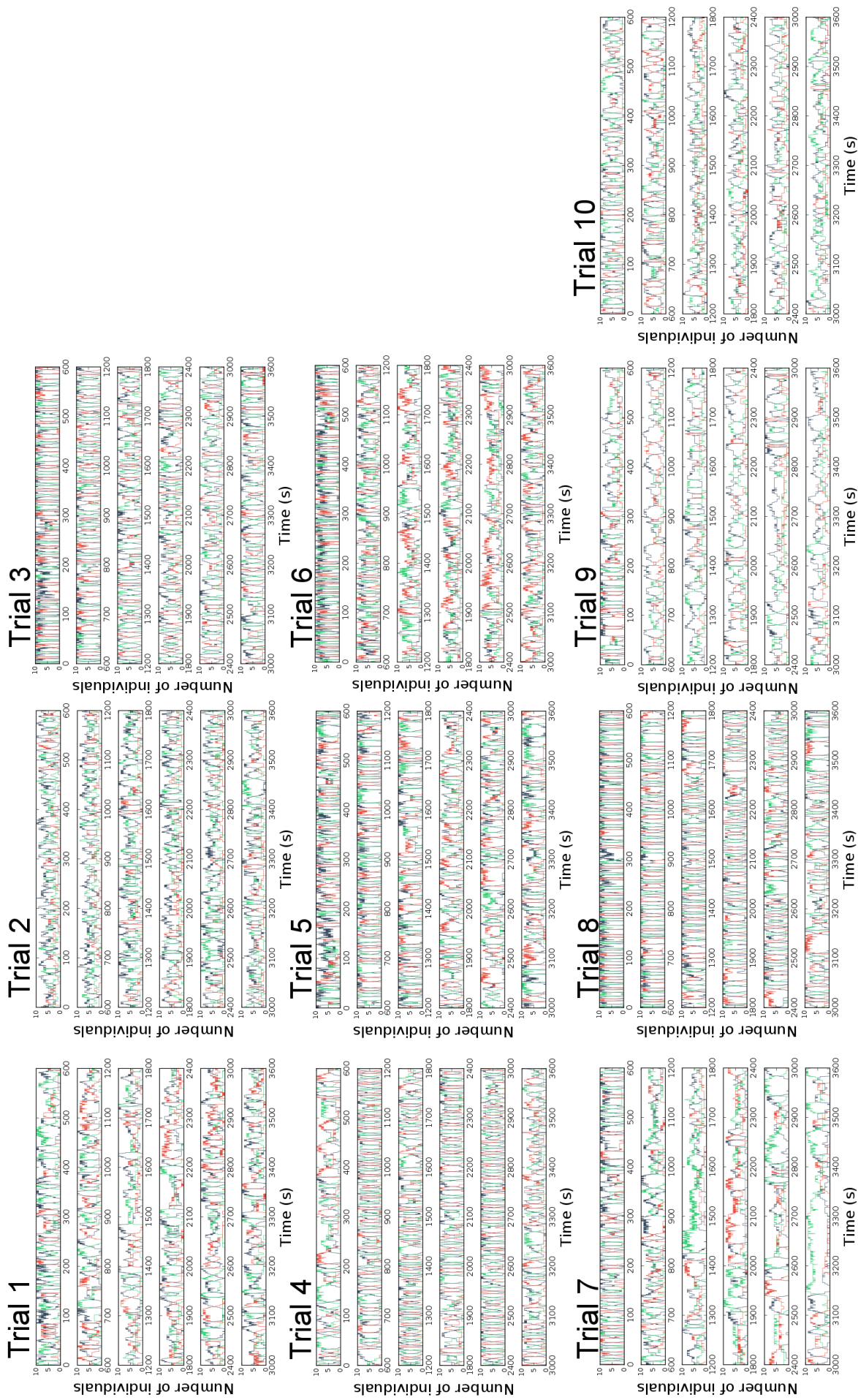


FIGURE 5.17 – **Landmark occupancy** for 10 trials of 10 AB zebrafish. For readability, time series are divided in 6 linked subplots. Y-axis reports the number of individuals. Green line represents individuals in the zone of interest (less than 25 cm away from the center of the landmark) of landmark 1, red line the individuals in the zone of interest of landmark 2 and blue line the individuals outside both zones of interest.

CHAPITRE 5. STRAIN DIFFERENCES IN THE COLLECTIVE BEHAVIOUR OF ZEBRAFISH (*DANIO RERIO*) IN HETEROGENEOUS ENVIRONMENT

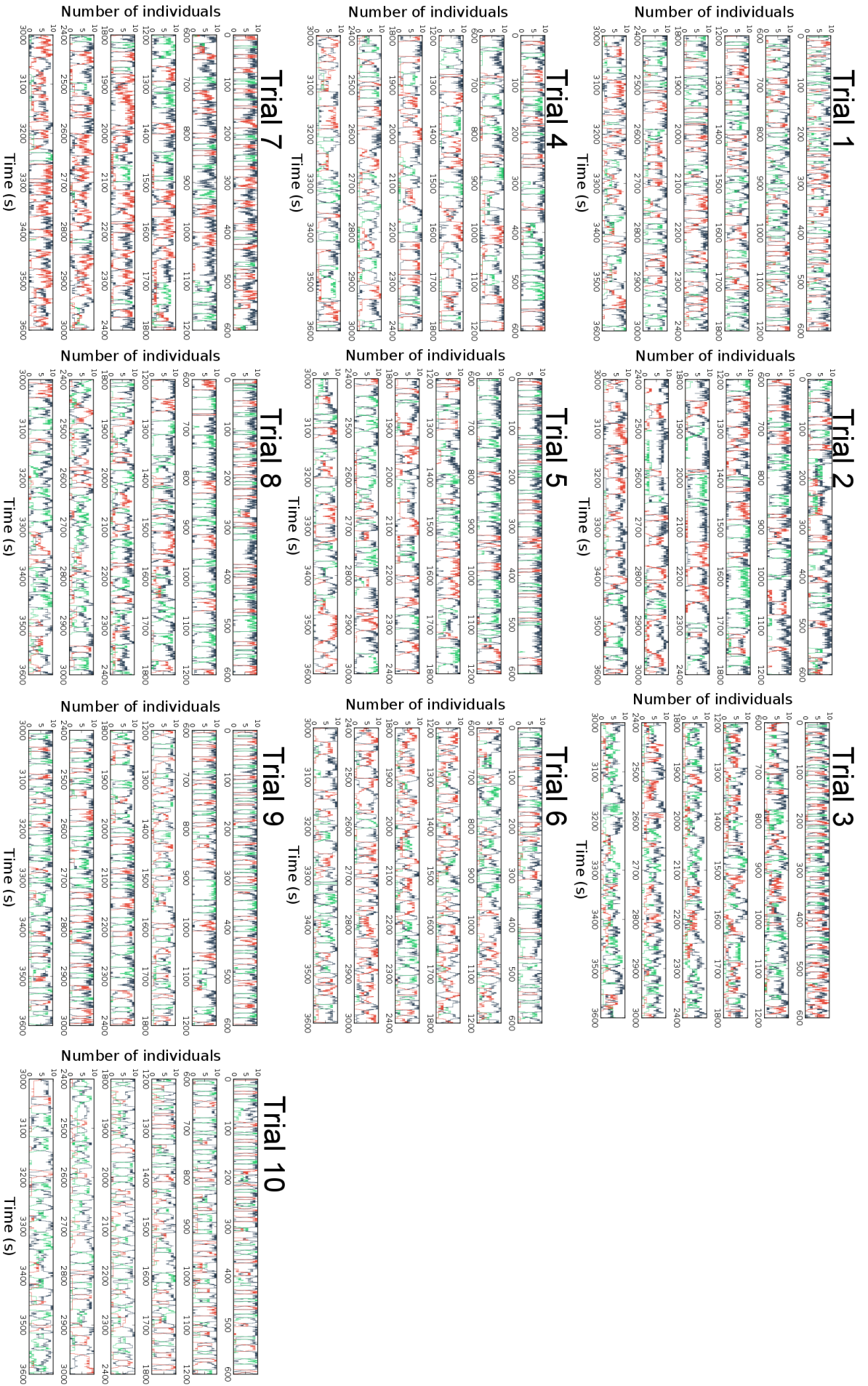


FIGURE 5.18 – Landmark occupancy for 10 trials of 10 TL zebrafish. For readability, time series are divided in 6 linked subplots. Y-axis reports the number of individuals. Green line represents individuals in the zone of interest (less than 25 cm away from the center of the landmark) of landmark 1, red line the individuals in the zone of interest of landmark 2 and blue line the individuals outside both zones of interest.

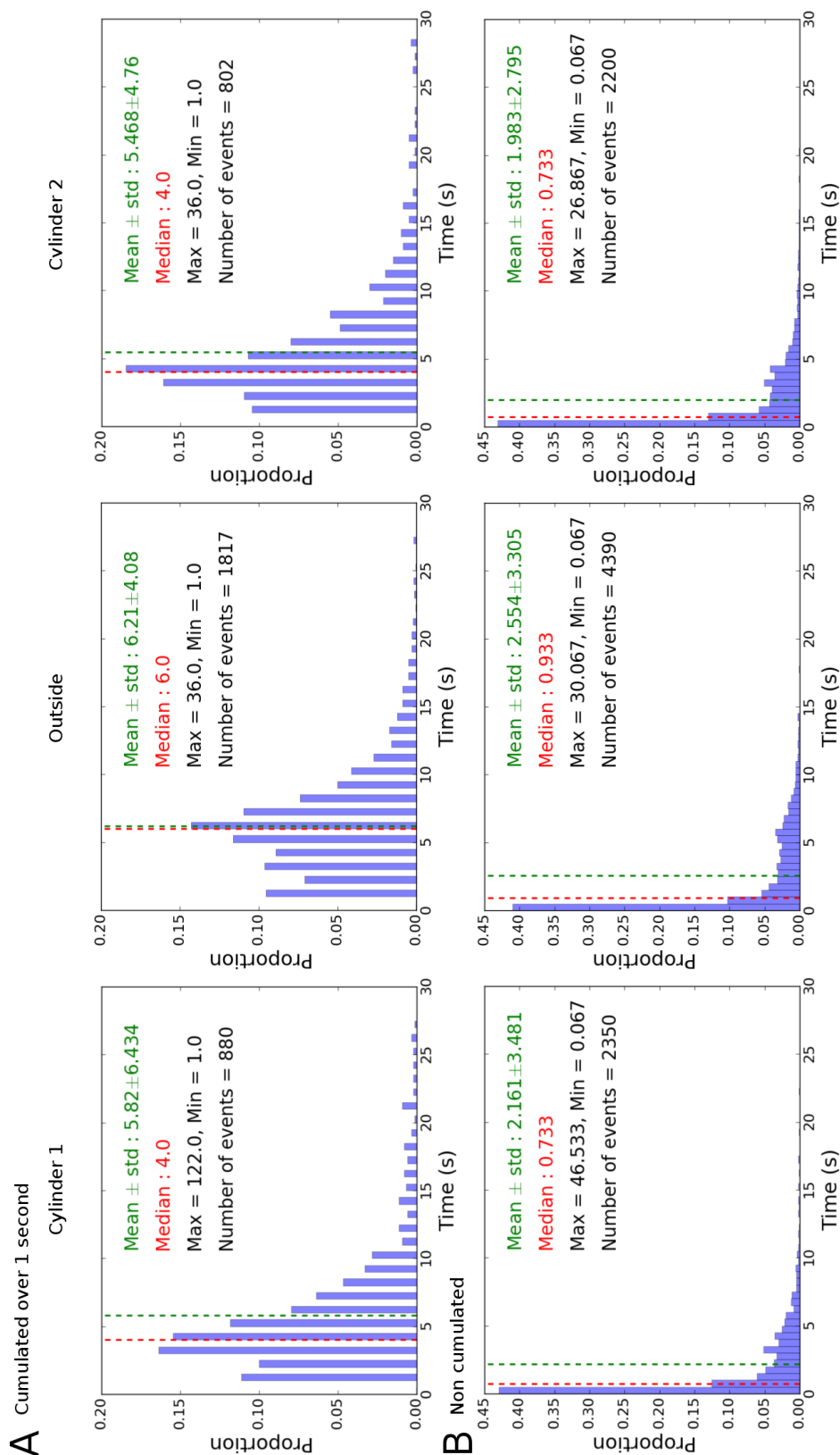


FIGURE 5.19 – **Comparison of the proportions of the durations of the majority events for AB zebrafish** (A) on cumulated data over 1 second; (B) on non cumulated data. This figure is related to the Figure 4 of the article. By cumulating the data over 1 second, we decrease strongly the noise. In each area, the median of the presence durations increases and reaches 4 seconds around cylinder 1 and 2 and 6 seconds outside.

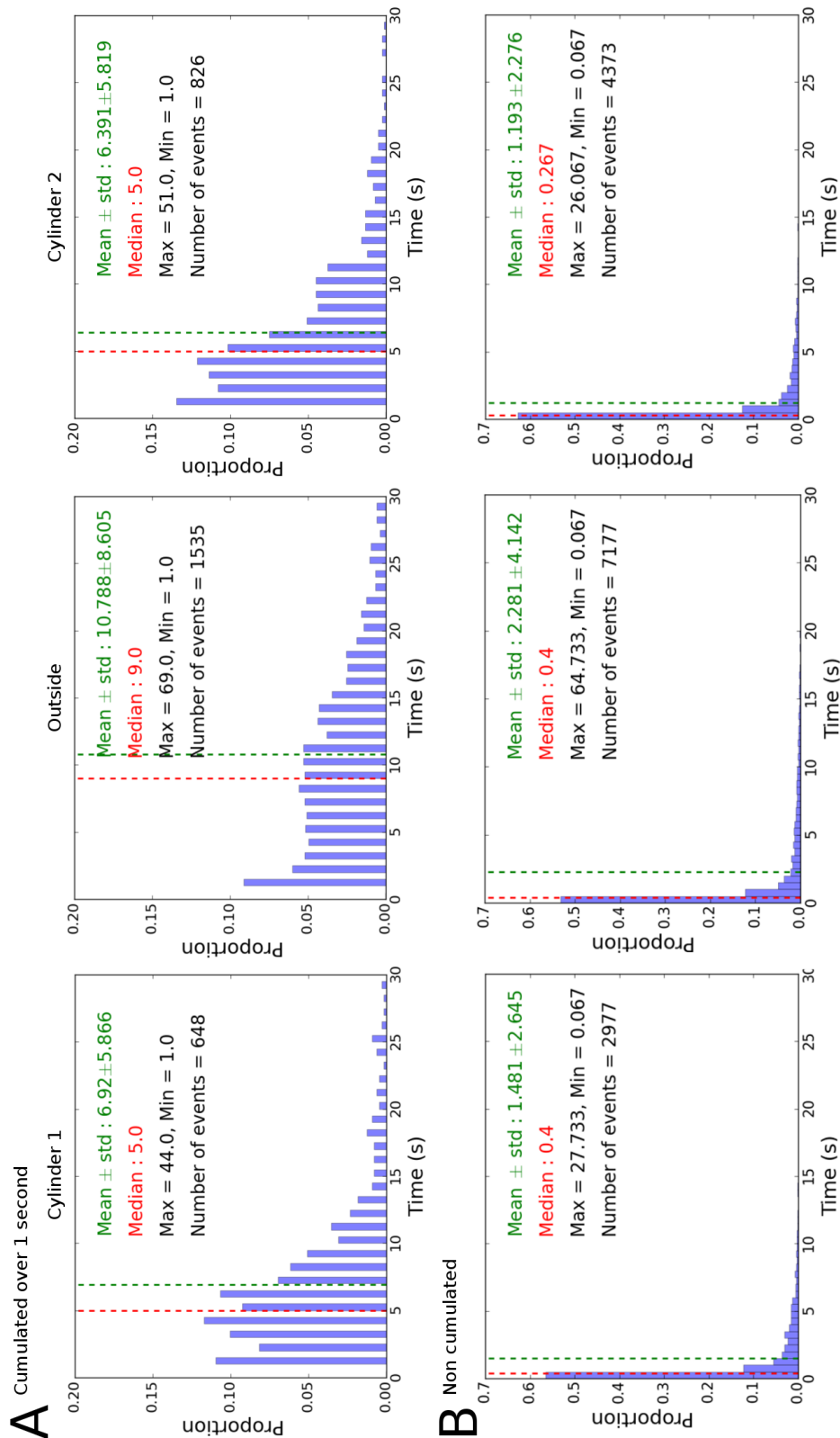


FIGURE 5.20 – Comparison of the proportions of the durations of the majority events for TL zebrafish (A) on cumulated data over 1 second; (B) on non cumulated data. This figure is related to the Figure 4 of the article. By cumulating the data over 1 second, we decrease strongly the noise. In each area, the median of the presence durations increases and reaches 5 seconds around cylinder 1 and 2 and to 9 seconds outside.

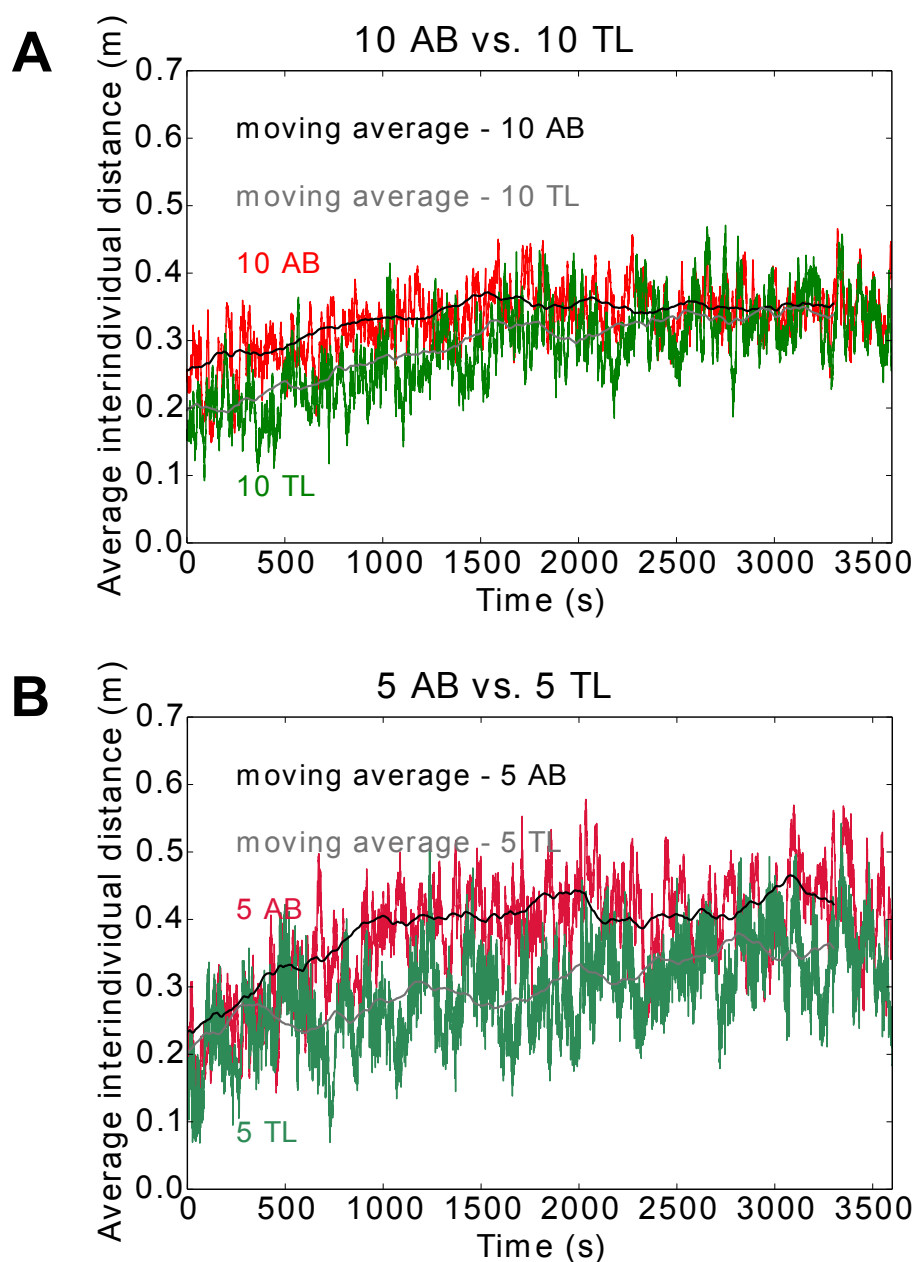


FIGURE 5.21 – **Time evolution of the average interindividual distance** (A) for 10 AB versus 10 TL fish (in the presence of cylinders). The red line is the average of 10 trials with groups of 10 AB zebrafish, the green line is the average of 10 trials with groups of 10 TL zebrafish; (B) for 5 AB versus 5 TL fish. The red line is the average of 10 trials with groups of 5 AB zebrafish, the green line is the average of 10 trials with groups of 5 TL zebrafish. The average interindividual distance for each condition shows an increase during the first 20 minutes and the reaching of a plateau. It has been calculated as the average of all distances between each couple of fish.

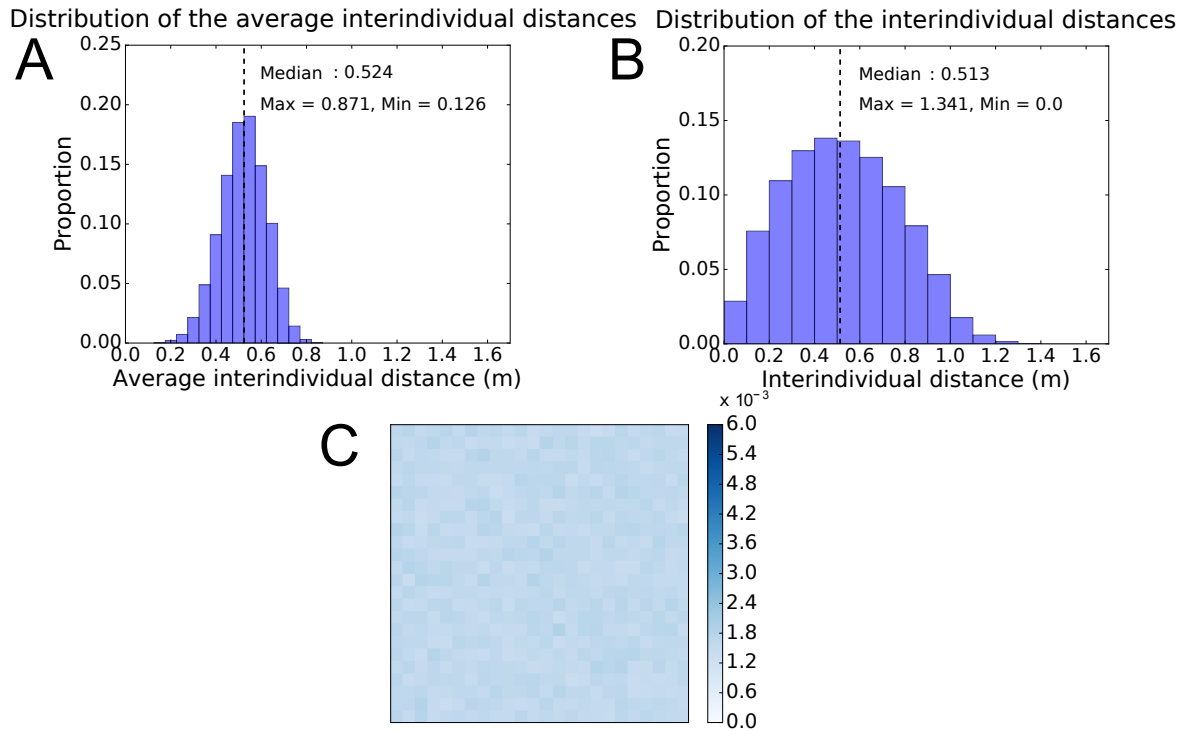


FIGURE 5.22 – **Randomised data of 5 agents for 10 trials** in a 100 cm x 100 cm arena with two cylinders. (A) The distribution of the average interindividual distances with randomised data can be compared with Fig. 2 (B) of the main article (The medians of the distributions of the average interindividual distances for 5 AB is 0.39m and for 5 TL is 0.30m). (B) The distribution of the interindividual distances with randomised data can be compared with Fig. 1 (C and D) of the main article (The medians of the distributions of the interindividual distances for 5 AB is 0.27m and for 5 TL is 0.12m). (C) The probability of presence of randomised data can be compared with Fig. 5 (C and D) of the main article.

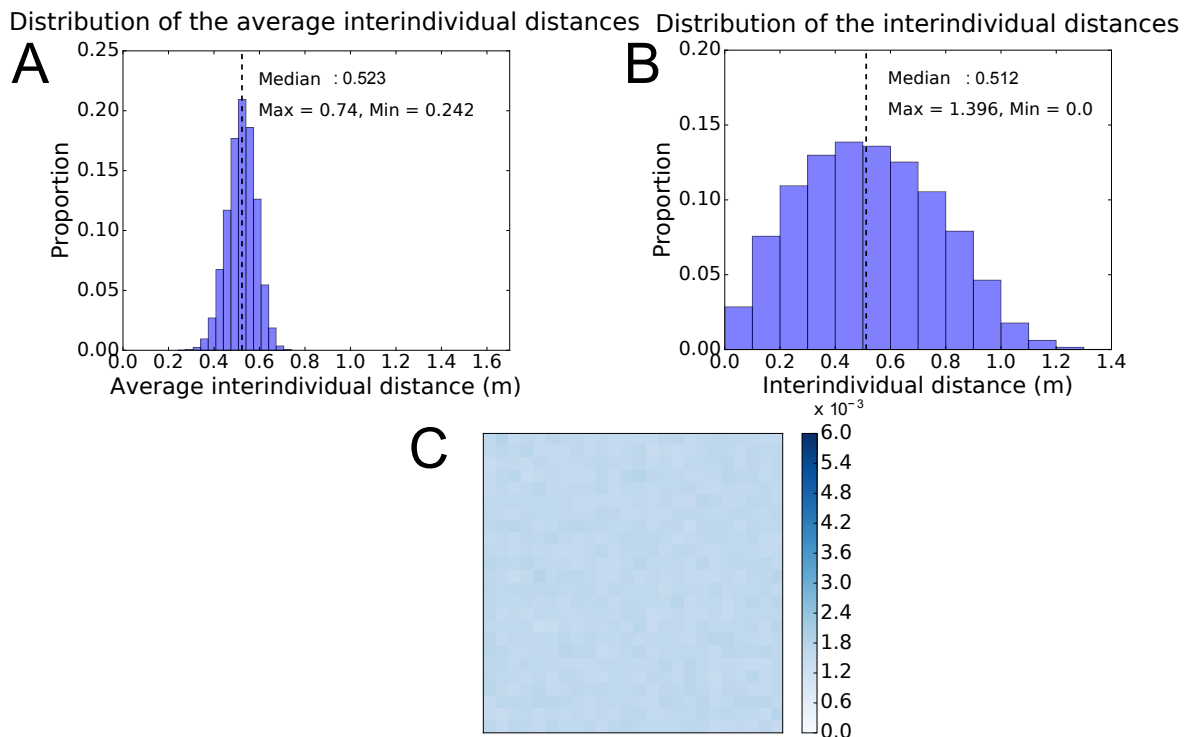


FIGURE 5.23 – **Randomised data of 10 agents for 10 trials** in a 100 cm x 100 cm arena with two cylinders. (A) The distribution of the average interindividual distances with randomised data can be compared with Fig. 2 (A) of the main article (The medians of the distributions of the average interindividual distances for 10 AB is 0.33m, for 10 TL is 0.29m). (B) The distribution of the interindividual distances with randomised data can be compared with Fig. 1 (A and B) of the main article (The medians of the distributions of the interindividual distances for 10 AB is 0.23m, for 10 TL is 0.14m). (C) The probability of presence of randomised data can be compared with Fig. 5 (A and B) of the main article.

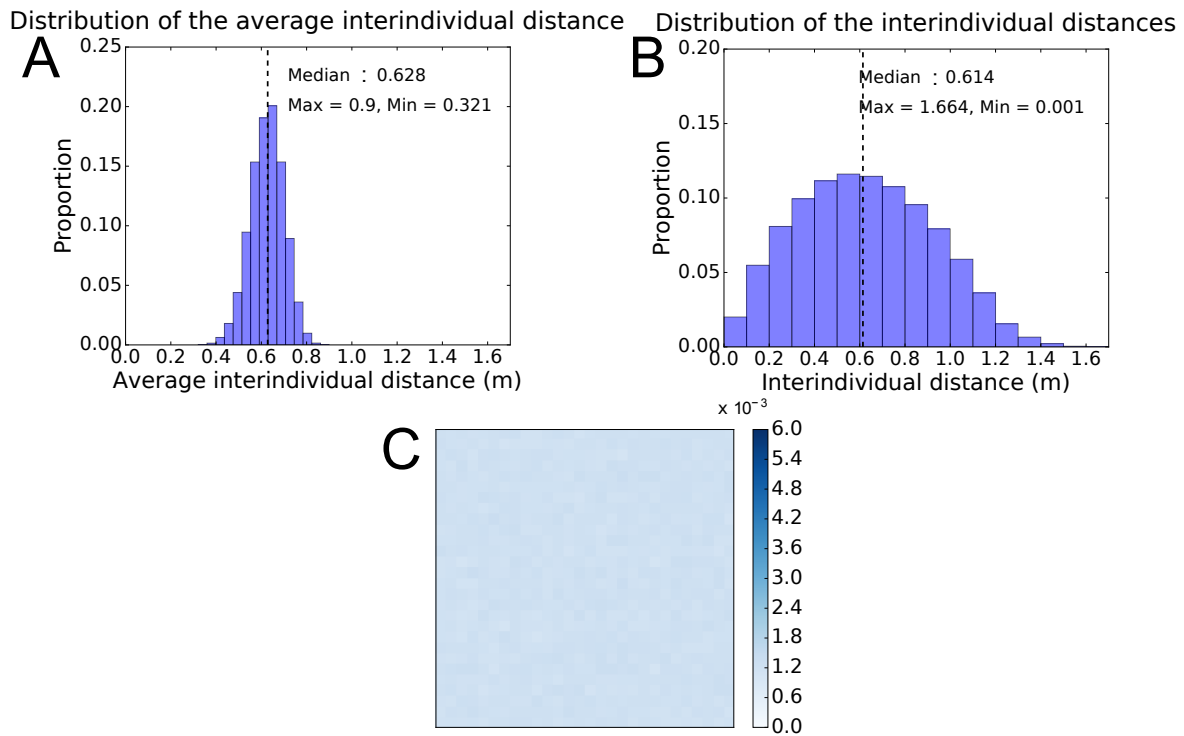


FIGURE 5.24 – **Randomised data of 10 agents for 10 trials** in a 120 cm x 120 cm arena with two disks. (A) The distribution of the average interindividual distances with randomised data can be compared with Fig. 4 of the main article (The medians of the distributions of the average interindividual distances for 10 AB : 0.45m and for 10 TL : 0.41m). (B) The distribution of the interindividual distances with randomised data can be compared with Fig. 3 (A and B) of the main article (The medians of the distributions of the interindividual distances for 10 AB : 0.35m and for 10 TL : 0.23m). (C) The probability of presence of randomised data can be compared with Fig. 6 (A and B) of the main article.

5.8 Références

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- Amé, J.-M., J. Halloy, C. Rivault, C. Detrain et J. L. Deneubourg. 2006, «Collegial decision making based on social amplification leads to optimal group formation», *Proceedings of the National Academy of Sciences*, vol. 103, n° 15, p. 5835–5840. [45](#), [46](#)
- Ame, J.-M., C. Rivault et J.-L. Deneubourg. 2004, «Cockroach aggregation based on strain odour recognition», *Animal behaviour*, vol. 68, n° 4, p. 793–801. [56](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini et collab.. 2008, «Interaction ruling animal collective behavior depends on topological rather than metric distance : Evidence from a field study», *Proceedings of the national academy of sciences*, vol. 105, n° 4, p. 1232–1237. [61](#)
- Becco, C., N. Vandewalle, J. Delcourt et P. Poncin. 2006, «Experimental evidences of a structural and dynamical transition in fish school», *Physica A : Statistical Mechanics and its Applications*, vol. 367, p. 487–493. [45](#)
- Beckers, R., J.-L. Deneubourg et S. Goss. 1992, «Trails and u-turns in the selection of a path by the ant *lasius niger*», *Journal of theoretical biology*, vol. 159, n° 4, p. 397–415. [46](#)
- Beckers, R., J.-L. Deneubourg, S. Goss et J. Pasteels. 1990, «Collective decision making through food recruitment», *Insectes sociaux*, vol. 37, n° 3, p. 258–267. [46](#)
- Branson, K., A. A. Robie, J. Bender, P. Perona et M. H. Dickinson. 2009, «High-throughput ethomics in large groups of drosophila», *Nature methods*, vol. 6, n° 6, p. 451–457. [61](#)
- Brousseau, D. J., J. A. Baglivo, A. Filipowicz, L. Seigo et C. Alt. 2002, «An experimental field study of site fidelity and mobility in the asian shore crab, *hemigrapsus sanguineus*», *Northeastern Naturalist*, vol. 9, n° 4, p. 381–390. [56](#)
- Buske, C. et R. Gerlai. 2011, «Shoaling develops with age in zebrafish (*danio rerio*)», *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, vol. 35, n° 6, p. 1409–1415. [58](#)
- Collignon, B., A. Séguret et J. Halloy. 2016, «A stochastic vision-based model inspired by zebrafish collective behaviour in heterogeneous environments», *Royal Society open science*, vol. 3, n° 1, p. 150473. [46](#)
- Conradt, L. et T. J. Roper. 2005, «Consensus decision making in animals», *Trends in ecology & evolution*, vol. 20, n° 8, p. 449–456. [45](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [56](#)

- Dankert, H., L. Wang, E. D. Hoopfer, D. J. Anderson et P. Perona. 2009, «Automated monitoring and analysis of social behavior in drosophila», *Nature methods*, vol. 6, n° 4, p. 297–303. [61](#)
- Detrain, C. et J.-L. Deneubourg. 2008, «Collective decision-making and foraging patterns in ants and honeybees», *Advances in insect physiology*, vol. 35, p. 123–173. [45](#)
- Dussutour, A., J.-L. Deneubourg, S. Beshers et V. Fourcassié. 2009, «Individual and collective problem-solving in a foraging context in the leaf-cutting ant *atta colombica*», *Animal cognition*, vol. 12, n° 1, p. 21–30. [45](#)
- Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan et D. M. Parichy. 2007, «Timing and plasticity of shoaling behaviour in the zebrafish, *danio rerio*», *Animal behaviour*, vol. 74, n° 5, p. 1269–1275. [45](#), [46](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [45](#), [56](#)
- Gerlai, R. 2014, «Social behavior of zebrafish : from synthetic images to biological mechanisms of shoaling», *Journal of neuroscience methods*, vol. 234, p. 59–65. [60](#)
- Guayasamin, O. 2013, «Personality matters : A quantitative comparison of asocial and social behaviors in the zebrafish (*danio rerio*)», . [56](#)
- Harcourt, J. L., G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Personality counts : the effect of boldness on shoal choice in three-spined sticklebacks», *Animal Behaviour*, vol. 77, n° 6, p. 1501–1505. [56](#)
- Hemelrijk, C. K. et H. Hildenbrandt. 2012, «Schools of fish and flocks of birds : their shape and internal structure by self-organization», *Interface focus*, p. rsfs20120 025. [45](#)
- Hemmings, C. 1966, «Olfaction and vision in fish schooling», *Journal of Experimental Biology*, vol. 45, n° 3, p. 449–464. [58](#)
- Herbert-Read, J. E., S. Krause, L. Morrell, T. Schaerf, J. Krause et A. Ward. 2013, «The role of individuality in collective group movement», dans *Proc. R. Soc. B*, vol. 280, The Royal Society, p. 20122564. [45](#)
- Herbert-Read, J. E., A. Perna, R. P. Mann, T. M. Schaerf, D. J. Sumpter et A. J. Ward. 2011, «Inferring the rules of interaction of shoaling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18 726–18 731. [45](#)
- Iovine, M. K. et S. L. Johnson. 2000, «Genetic analysis of isometric growth control mechanisms in the zebrafish caudal fin», *Genetics*, vol. 155, n° 3, p. 1321–1329. [58](#)
- Jeanson, R., A. Dussutour et V. Fourcassié. 2014, «Key factors for the emergence of collective decision in invertebrates», *Decision-making in invertebrates*, p. 133. [45](#)

- Katrak, G. et S. Dittmann. 2011, «Site specific distribution of the mud shore crab *helograpsus haswellianus* in temperate wetlands», *Wetlands ecology and management*, vol. 19, n° 5, p. 433–448. [56](#)
- Kistler, C., D. Hegglin, H. Würbel et B. König. 2011, «Preference for structured environment in zebrafish (*danio rerio*) and checker barbs (*puntius oligolepis*)», *Applied Animal Behaviour Science*, vol. 135, n° 4, p. 318–327. [45](#)
- Lange, M., F. Neuzeret, B. Fabreges, C. Froc, S. Bedu, L. Bally-Cuif et W. H. Norton. 2013, «Inter-individual and inter-strain variations in zebrafish locomotor ontogeny», *PloS one*, vol. 8, n° 8, p. e70172. [58](#)
- Lau, B. Y., P. Mathur, G. G. Gould et S. Guo. 2011, «Identification of a brain center whose activity discriminates a choice behavior in zebrafish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 6, p. 2581–2586. [60](#)
- Leblond, C. et S. G. Reebbs. 2006, «Individual leadership and boldness in shoals of golden shiners (*notemigonus crysoleucas*)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [57](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danio-nin fishes, including the zebrafish *danio rerio*», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [46](#)
- Michelena, P., A. M. Sibbald, H. W. Erhard et J. E. McLeod. 2009, «Effects of group size and personality on social foraging : the distribution of sheep across patches», *Behavioral Ecology*, vol. 20, n° 1, p. 145–152. [57](#)
- Miller, N., S. Garnier, A. T. Hartnett et I. D. Couzin. 2013, «Both information and social cohesion determine collective decisions in animal groups», *Proceedings of the National Academy of Sciences*, vol. 110, n° 13, p. 5263–5268. [45](#), [46](#)
- Miller, N. et R. Gerlai. 2007, «Quantification of shoaling behaviour in zebrafish (*danio rerio*)», *Behavioural brain research*, vol. 184, n° 2, p. 157–166. [61](#)
- Miller, N. Y. et R. Gerlai. 2011, «Shoaling in zebrafish : what we don't know», *Reviews in the Neurosciences*, vol. 22, n° 1, p. 17–25. [61](#)
- Millot, S., M.-L. Bégout et B. Chatain. 2009, «Risk-taking behaviour variation over time in sea bass *dicentrarchus labrax* : effects of day–night alternation, fish phenotypic characteristics and selection for growth», *Journal of fish biology*, vol. 75, n° 7, p. 1733–1749. [57](#)
- Morgan, M. 1988, «The effect of hunger, shoal size and the presence of a predator on shoal cohesiveness in bluntnose minnows, *pimephales notatus rafinesque*», *Journal of Fish Biology*, vol. 32, n° 6, p. 963–971. [58](#)

- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [46](#)
- Oliveira, R. F. 2014, «Mind the fish : zebrafish as a model in cognitive social neuroscience», *Frontiers in neural circuits*. [46](#)
- Parichy, D. M. 2015, «Advancing biology through a deeper understanding of zebrafish ecology and evolution», *ELife*, vol. 4, p. e05 635. [46](#)
- Parrish, J. K., S. V. Viscido et D. Grünbaum. 2002, «Self-organized fish schools : an examination of emergent properties», *The biological bulletin*, vol. 202, n° 3, p. 296–305. [45](#)
- Partridge, B. L. et T. J. Pitcher. 1980, «The sensory basis of fish schools : relative roles of lateral line and vision», *Journal of Comparative Physiology*, vol. 135, n° 4, p. 315–325. [58](#)
- Petit, O. et R. Bon. 2010, «Decision-making processes : the case of collective movements», *Behavioural Processes*, vol. 84, n° 3, p. 635–647. [45](#)
- Pita, D., B. A. Moore, L. P. Tyrrell et E. Fernández-Juricic. 2015, «Vision in two cyprinid fish : implications for collective behavior», *PeerJ*, vol. 3, p. e1113. [58](#)
- Plaut, I. 2000, «Effects of fin size on swimming performance, swimming behaviour and routine activity of zebrafish danio rerio», *Journal of Experimental Biology*, vol. 203, n° 4, p. 813–820. [58](#)
- Pritchard, V. L., J. Lawrence, R. K. Butlin et J. Krause. 2001, «Shoal choice in zebrafish, danio rerio : the influence of shoal size and activity», *Animal Behaviour*, vol. 62, n° 6, p. 1085–1088. [46](#)
- Radakov, D. V. 1973, «Schooling in the ecology of fish», . [45](#)
- Rehnberg, B. et R. Smith. 1988, «The influence of alarm substance and shoal size on the behaviour of zebra danios, brachydanio rerio (cyprinidae)», *Journal of Fish Biology*, vol. 33, n° 1, p. 155–163. [58](#)
- Reiser, M. 2009, «The ethomics era?», *Nature methods*, vol. 6, n° 6, p. 413–414. [61](#)
- Risner, M. L., E. Lemerise, E. V. Vukmanic et A. Moore. 2006, «Behavioral spectral sensitivity of the zebrafish (danio rerio)», *Vision research*, vol. 46, n° 17, p. 2625–2635. [46](#)
- Saverino, C. et R. Gerlai. 2008, «The social zebrafish : behavioral responses to conspecific, heterospecific, and computer animated fish», *Behavioural brain research*, vol. 191, n° 1, p. 77–87. [60](#)
- SEGHERS, B., P. SHAW et G. Carvalho. 1995, «The behavioral diversity and evolution of guppy, poecilia reticulata, populations in trinidad», *Advances in the Study of Behavior*, vol. 24, p. 155. [57](#)
- Sison, M. et R. Gerlai. 2010, «Associative learning in zebrafish (danio rerio) in the plus maze», *Behavioural brain research*, vol. 207, n° 1, p. 99–104. [45](#), [46](#)

- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, *danio rerio*», *Biological Reviews*, vol. 83, n° 1, p. 13–34. [46](#)
- Strandburg-Peshkin, A., C. R. Twomey, N. W. Bode, A. B. Kao, Y. Katz, C. C. Ioannou, S. B. Rosenthal, C. J. Torney, H. S. Wu, S. A. Levin et collab.. 2013, «Visual sensory networks and effective information transfer in animal groups», *Current Biology*, vol. 23, n° 17, p. R709–R711. [61](#)
- Sueur, C., J.-L. Deneubourg et O. Petit. 2011, «From the first intention movement to the last joiner : macaques combine mimetic rules to optimize their collective decisions», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 278, n° 1712, p. 1697–1704. [45](#)
- Sullivan, M., C. Lawrence et D. Blache. 2016, «Why did the fish cross the tank? objectively measuring the value of enrichment for captive fish», *Applied Animal Behaviour Science*, vol. 174, p. 181–188. [45](#)
- Sumpter, D. J., N. Zabzina et S. C. Nicolis. 2012, «Six predictions about the decision making of animal and human groups», *Managerial and decision economics*, vol. 33, n° 5-6, p. 295–309. [45](#)
- Suriyampola, P. S. et P. K. Eason. 2014, «A field study investigating effects of landmarks on territory size and shape», *Biology letters*, vol. 10, n° 4, p. 20140009. [45](#)
- Suriyampola, P. S. et P. K. Eason. 2015, «The effects of landmarks on territorial behavior in a convict cichlid, *amatitlania siquia*», *Ethology*, vol. 121, n° 8, p. 785–792. [45](#)
- Suriyampola, P. S., D. S. Shelton, R. Shukla, T. Roy, A. Bhat et E. P. Martins. 2016, «Zebrafish social behavior in the wild», *Zebrafish*, vol. 13, n° 1, p. 1–8. [46](#)
- Thorrold, S. R., C. Latkoczy, P. K. Swart et C. M. Jones. 2001, «Natal homing in a marine fish meta-population», *Science*, vol. 291, n° 5502, p. 297–299. [56](#)
- Tunstrøm, K., Y. Katz, C. C. Ioannou, C. Huepe, M. J. Lutz et I. D. Couzin. 2013, «Collective states, multistability and transitional behavior in schooling fish», *PLoS Comput Biol*, vol. 9, n° 2, p. e1002915. [45](#)
- Ward, A. J., J. E. Herbert-Read, D. J. Sumpter et J. Krause. 2011, «Fast and accurate decisions through collective vigilance in fish shoals», *Proceedings of the National Academy of Sciences*, vol. 108, n° 6, p. 2312–2315. [45](#), [46](#)
- Watanabe, M., M. Iwashita, M. Ishii, Y. Kurachi, A. Kawakami, S. Kondo et N. Okada. 2006, «Spot pattern of leopard danio is caused by mutation in the zebrafish connexin41. 8 gene», *EMBO reports*, vol. 7, n° 9, p. 893–897. [58](#)
- Wolfe, B. W. et C. G. Lowe. 2015, «Movement patterns, habitat use and site fidelity of the white croaker (*genyonemus lineatus*) in the palos verdes superfund site, los angeles, california», *Marine environmental research*, vol. 109, p. 69–80. [56](#)

*CHAPITRE 5. STRAIN DIFFERENCES IN THE COLLECTIVE BEHAVIOUR OF
ZEBRAFISH (DANIO RERIO) IN HETEROGENEOUS ENVIRONMENT*

Wright, D., L. B. Rimmer, V. L. Pritchard, R. Butlin et J. Krause. 2003, «Inter and intra-population variation in shoaling and boldness in the zebrafish (danio rerio)», *Journal of Fish Biology*, vol. 63, n° 1, p. 258–259. [57](#)

Wright, D., A. Ward, D. Croft et J. Krause. 2006, «Social organization, grouping, and domestication in fish», *Zebrafish*, vol. 3, n° 2, p. 141–155. [57](#)

Chapitre 6

Loose social organisation of AB strain zebrafish groups in a two-patch environment

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In review

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6.1 Résumé

Nous analysons les déplacements collectifs, de sept tailles de population (1, 2, 3, 5, 7, 10 et 20 individus) de zebrafish (*Danio rerio*) provenant de la souche AB, dans un environnement contraint constitué de deux chambres carrées identiques connectées par un couloir. Ce système expérimental n'est pas sans rappeler les environnements parcellaires que l'on trouve dans la nature. Nous relevons ainsi les positions tout en conservant les identités des poissons et développons par la même occasion des outils d'analyse des comportements du groupe ainsi que des individus. Tout d'abord, nous avons remarqué que la taille de la population a un effet direct sur le comportement de chaque individu, la cohésion du groupe, l'affinité entre les individus et les transitions entre les deux chambres. Enfin, lors des départs collectifs d'une quelconque chambre, nous montrons que l'ordre de sortie des poissons correspond à une organisation topologique antérieure au départ. Cette organisation spatiale apparaît quelques secondes avant le départ collectif. Ces résultats apportent ainsi de nouvelles preuves dans l'organisation spatiale des groupes d'animaux et de l'influence de la taille des populations sur les comportements individuels et collectifs dans des environnements parcellaires.

6.2 Abstract

We explore the collective behaviours of 7 group sizes : 1, 2, 3, 5, 7, 10 and 20 AB zebrafish (*Danio rerio*) in a constraint environment composed of two identical squared rooms connected by a corridor. This simple set-up is similar to a natural patchy environment. We track the positions and the identities of the fish and compute the metrics at the group and at the individual levels. First, we show that the density affects the behaviour of each individual in a group, the cohesion of the groups, the preferential interactions and the transition dynamics between the two rooms. Second, during collective departures, we show that the rankings of exit correspond to the topological organisations of the fish prior to their collective departure with no leadership. This spatial organisation appears in the group a few seconds before a collective departure. These results provide new evidences on the spatial organisation of the groups and the effect of the density on individual and collective behaviours in a patchy environment.

6.3 Introduction

Across the collective behaviours observed in animals, collective movements [Engeszer et collab. \[2007\]](#); [Hemelrijk et Hildenbrandt \[2012\]](#); [Herbert-Read et collab. \[2011\]](#); [Parrish et collab. \[2002\]](#); [Petit et Bon \[2010\]](#); [Radakov \[1973\]](#); [Sueur et collab. \[2011a,b\]](#), nest site

selections [Amé et collab. \[2006\]](#); [Dahlbom et collab. \[2011\]](#); [Franks et collab. \[2002\]](#); [Rieucau et collab. \[2010\]](#) and site transitions [Harcourt et collab. \[2009\]](#) have been evidenced in many species. In the latter case, the animals alone or in group face several alternatives and transit between them. The study of these transitions relies on decision-making processes and individual or collective preferences for environmental [Conradt et Roper \[2005\]](#) or group members characteristics [Engeszer et collab. \[2007, 2004\]](#); [Hoare et collab. \[2004\]](#); [Pritchard et collab. \[2001\]](#) like leadership [Couzin et collab. \[2005\]](#), motion [Bourjade et collab. \[2009\]](#) or behaviour, for example bold and shy individuals [Dahlbom et collab. \[2011\]](#); [Leblond et Reeb \[2006\]](#).

Numerous animal species have been observed in different sorts of constraint setups or mazes to study collective movement from one site to another : corridor type [Engeszer et collab. \[2007, 2004\]](#); [Pettersson et Brönmark \[1993\]](#), Y-maze [Ward et collab. \[2011\]](#), T-maze [Kistler et collab. \[2011\]](#) or Plus-maze [Miller et collab. \[2013\]](#); [Sison et Gerlai \[2010\]](#). Such constraint set-ups engage the animals to transit alone or in group from site to site and allow the observation of leadership [Bourjade et collab. \[2015\]](#); [Ward et collab. \[2013\]](#), initiation of group movements [Bourjade et collab. \[2009\]](#); [Rosenthal et collab. \[2015\]](#); [Ward et collab. \[2013\]](#), followers organisations [Ward et collab. \[2013\]](#), pre-departure behaviours [Bourjade et collab. \[2015, 2009\]](#) and sites transitions [Harcourt et collab. \[2009\]](#); [Nakayama et collab. \[2012a, 2011\]](#). In these latter cases the authors studied the transitions from one site to the other of one and two fish separated by a transparent partition (*Gasterosteus aculeatus* and *Sciaenops ocellatus*). Although such experimental procedure provided evidence of different leader/follower behaviour in fish, they prevent the fish from direct interactions between each other during the departures.

Studies performed with groups of fish swimming together have evidenced that the group density can impact swimming behaviours with variety of results. [Becco et collab. \[2006\]](#); [Herbert-Read et collab. \[2013\]](#); [Tunstrøm et collab. \[2013\]](#) showed that the speed, the turning speed, the nearest neighbour distances, the milling or the alignment are affected by the number of group members. The authors present opposite results depending on the species : increasing the group size of *Oreochromis niloticus* (330 and 905 fish), makes stronger alignments [Becco et collab. \[2006\]](#), when for *Notemigonus crysoleucas* (30, 70, 150 and 300 fish) alignments decrease [Tunstrøm et collab. \[2013\]](#).

Rather than investigating the influence of the group density on the swimming characteristic of the group, here, we focus on the collective movements between two environmental patches. In particular, we would like to characterise the dynamics of departure during sites transitions for several group densities (1, 2, 3, 5, 7, 10 and 20 individuals) of AB zebrafish swimming in a constraint environment. Zebrafish are a gregarious vertebrate model organisms often used in behavioural studies [Norton et Bally-Cuif \[2010\]](#); [Oliveira \[2014\]](#).

In the laboratory as much as in the nature, the zebrafish behave in groups [Engeszer et collab. \[2007\]](#); [McClure et collab. \[2006\]](#); [Spence et collab. \[2008\]](#). They are native to the Indian sub-continent and live in small groups or in big shoals of several hundreds of fish depending on the region and the water or the environmental features (temperature, pH, human activity, predators, ...) [Parichy \[2015\]](#); [Pritchard et collab. \[2001\]](#); [Suriyampola et collab. \[2016\]](#). Zebrafish live in a wide variability of habitats with varying structural complexities [Arunachalam et collab. \[2013\]](#); [Suriyampola et collab. \[2016\]](#) (from river channels, irrigation canals to beels) and we based our experimental method on the observations of fish swimming in a constraint set-up composed of two identical squared rooms connected by a long corridor evoking irrigation channels that go through and between the fields [Spence et collab. \[2006\]](#) and patchy environments [Wiens \[1976\]](#).

We showed in a previous study that zebrafish transit from one landmark to another one in an open environment during trials of one hour [Séguret et collab. \[2016\]](#). Moreover, we showed that groups of fish were swimming along the border of the tank and thus had a strong thigmotactic tendency [Collignon et collab. \[2016\]](#). Here, we introduce a new type of set-up to study group departures from an area, group transitions and social structures in zebrafish. We vary the density of the group to see how the zebrafish will face this environment and adapt their individual and group behaviours. We also perform trials of one hour that allow to study a large number of repetitive transitions.

6.4 Results

6.4.1 From the individual characteristics to pair interactions

The results presented in this paragraph focus on individual measures in 6 group sizes (1, 2, 3, 5, 7 and 10 fish).

First, we study the change of the group structure according to the location and group density by measuring the inter-individual distances between each pair of individuals. As the tracking software is able to individually recognise the different group members during the entire experiment, we were able to measure the distance between each specific pair of fish from the beginning to the end of the observation period. These distances are presented in figures [S6.11](#), [S6.12](#) and [S6.13](#) of the appendix that visually represent the median distances between the group members (all pairs of fish) in room 1, room 2 and the corridor for all group sizes (2, 3, 5, 7 and 10 zebrafish) and trials (12). Figure [6.1](#) shows the boxplots of these median distances between pairs of fish. Thus, the boxplots for 2 fish consists of 12 medians (12 x 1 couple), for 3 fish 36 medians (12 x 3 couples), for 5 fish 120 medians (12 x 10 couples), for 7 fish 252 medians (12 x 21 couples) and for 10 fish 540 medians (12 x 45 couples).

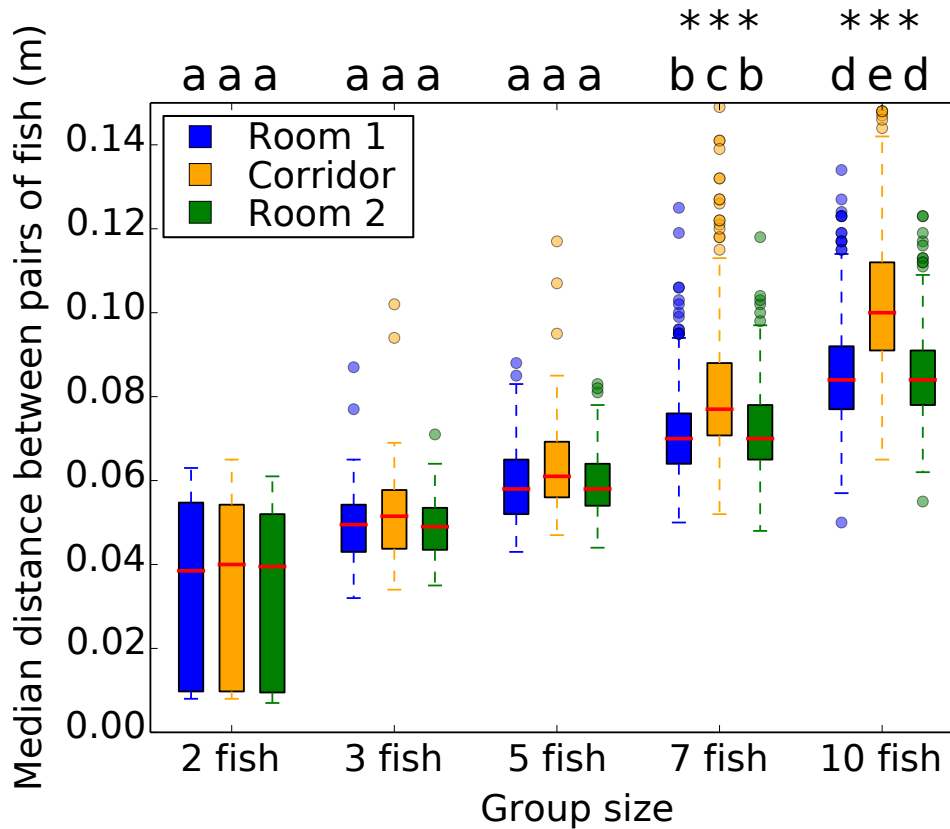


FIGURE 6.1 – **Boxplots of the medians of the distance distribution between all respective pairs of zebrafish** (A) in the room 1, (B) in the room 2 and (C) in the corridor. The red line is the median. The bigger the population, the larger the distances between fish pairs. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non significant.

Again, we compared the distributions of the median distances between the pairs focusing on each area (room 1, room 2 and corridor) or each group density. In each area, the median distances do not significantly differ between groups of 2, 3 or 5 fish. On the contrary, group density of 7 fish show significantly larger distance from each other as well as fish in groups of 10 that differ from all other group densities (Kruskall-Wallis $p < 0.001$, Tukey's honest significant difference criterion, $p > 0.05$ between groups of 2, 3 and 5 fish, $p < 0.001$ in all pair comparisons with groups of 7 and 10). Then, we compared for each group density the distribution of the distances according to the location of the fish. In this case, the distributions between both rooms are not significantly different for all group densities but they are significantly different between the corridor and the rooms 1 or 2 for group densities of 5, 7 and 10 individuals. The structure of the group is thus influenced by both the group density and the location of the fish in their environment.

6.4.2 Oscillations and collective departures

In this section, we characterise the collective behaviour of the fish. In particular, we focus our investigation on the oscillations between both rooms and the collective departure

dynamics of the groups. First, we studied the repartition of the fish among the two rooms. Approximately 70% of the positions of the fish were detected in the rooms, independently of the group density (Figure 6.19). In the Figure 6.2, we show that 80% of the time, less than 20% or more than 80% of the whole group is detected in the room 1. This result highlights that, as expected for a social species, the fish are not spread homogeneously in the two rooms but aggregate collectively in the patches, with only few observations of homogeneous repartition in both rooms. However, this analysis also show that the proportion of observation with equal repartition between both rooms (40-60%) increases with the density of the group. Thus, even if they are mainly observed together, fish in large group have a higher tendency to segregate in two groups. We show that the frequencies of observations for the proportions of 80 to 100% of the whole group in the room 1 are higher than 50% for all densities, except for 10 and 20 fish. For each trial, we defined the room 1 as the starting room where we let the fish acclimatize during 5 minutes in a transparent perspex cylinder. This may explain the observed bias of presence in favour of room 1 that may be a consequence of longer residence time at the beginning of the trials.

Then, since the fish are observed most of the time forming one group in one of the two rooms, we studied the transitions of the majority of fish between the two patches during the whole experiment. In the Figure 6.3, we plot the median numbers of transitions between both rooms (see Figure 6.20 and Table 6.2 (D) of the appendix for the plot of the means of the numbers of transitions and their standard deviations in a table). We identify three categories of transitions. *One-by-one transitions* occur when the fish transit one by one from one room to the other, *Collective transitions* appear when the group transit between both rooms through the corridor and *Collective U-turns* occur when the group go back to the previous room. For 1 zebrafish, the *One-by-one transitions* and *Collective transitions* do not make sense, thus we created another category called *All transitions*. This last category is the sum of the *One-by-one transitions* and the *Collective transitions* for group density experiments of 2, 3, 5, 7, 10 and 20 fish, for the experiments with a unique fish *All transitions* mean every kind of transitions except *U-turns*. Bigger group densities makes the number of *Collective U-turns*, *Collective transitions* and *All transitions* decrease and the number of *One-by-one transitions* increase. For the transitions (collective, one-by-one and all), this tendency intensifies for bigger groups of 10 and 20 zebrafish. Also, for groups of 3 zebrafish, there are less *Collective transitions* (as well as *All transitions*) than for groups of 2, 5 and 7 zebrafish. *U-turns* and *Collective U-turns* stay rare and are very stable for all group densities and their highest mean numbers are reached for group of 2 and 3 zebrafish. *One-by-one transitions* are as well very rare for small groups and increase when the group density reaches 10 zebrafish.

For each group density, we compared with a Kruskal-Wallis test the distributions of the number of transitions (Collective, One-by-one and U-turns) and found : for 1 fish, $df = 2$,

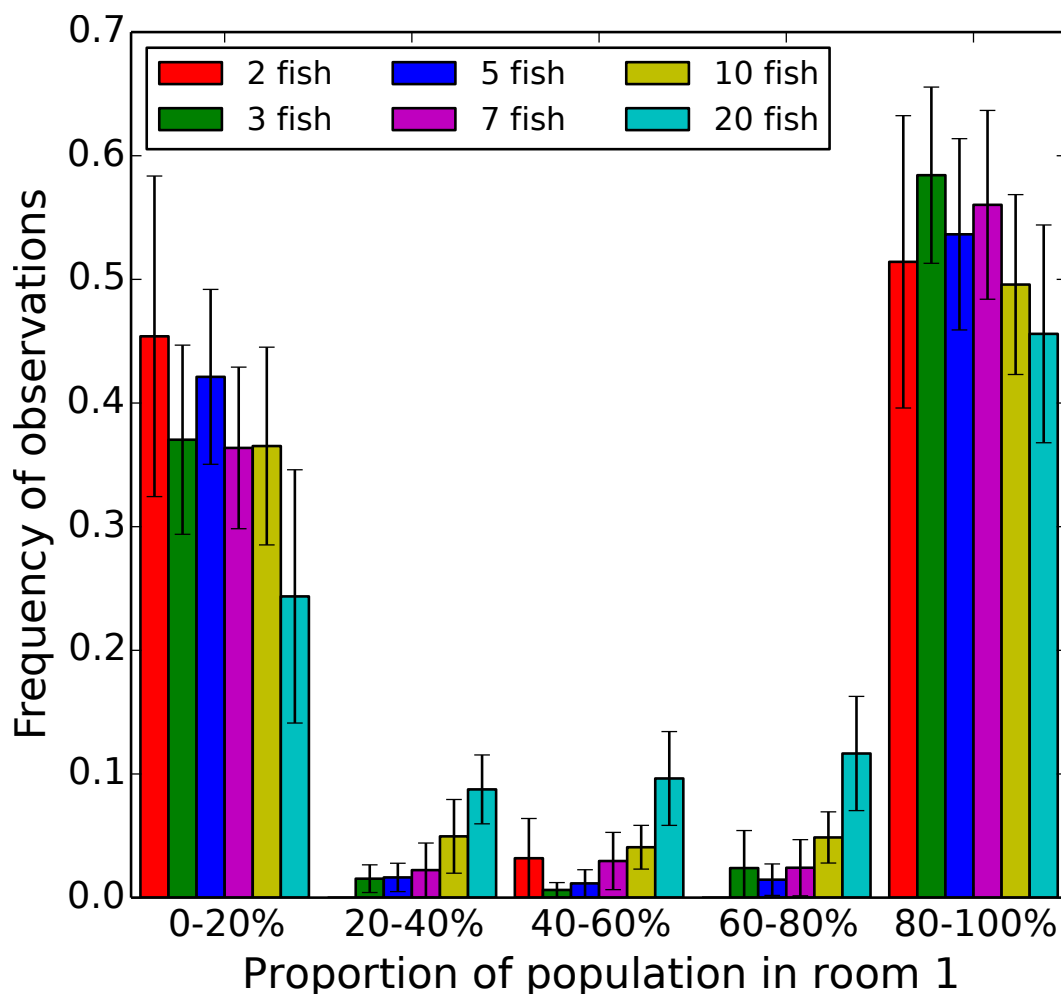


FIGURE 6.2 – **Frequency of the proportion of the population in room 1.** Almost 35% of the time, 0 to 20% of the population is present in the room 1 when almost 50% of the times, 80 to 100% of the population is in the room 1. Focusing on more equal repartition of the fish between the rooms (40 to 60% of the population), larger populations lead to higher frequency of group splitting.

Chi-sq = 31.62 $p < 0.001$; for 2 fish, df = 2, Chi-sq = 30.76, $p < 0.001$; for 3 fish, df = 2, Chi-sq = 30.94, $p < 0.001$; for 5 fish, df = 2, Chi-sq = 30.41, $p < 0.001$; for 7 fish, df = 2, Chi-sq = 30.54, $p < 0.001$; for 10 fish, df = 2, Chi-sq = 19.22, $p < 0.001$ and for 20 fish, df = 2, Chi-sq = 18.36, $p < 0.001$. For each group density, we show that at least one of the distributions is significantly different from the others. The Tukey's honest significant difference criterion shows that : all the distributions are significantly different ($p < 0.05$) except in groups of 10 individuals between *Collective U-turns* and *One-by-one transitions* and in groups of 20 individuals between *Collective U-turns* and *Collective transitions*.

As most of the transitions occur in groups, we analysed the dynamics of collective departure from the rooms. Thus, for each collective departure of the fish, defined as the whole group leaving one of the resting sites for the corridor towards the other one, we identified the ranking of exit of each fish and also their distance from the first fish leaving the room (i.e. defined as the initiator). Figure 6.4 represents the normalised contingency

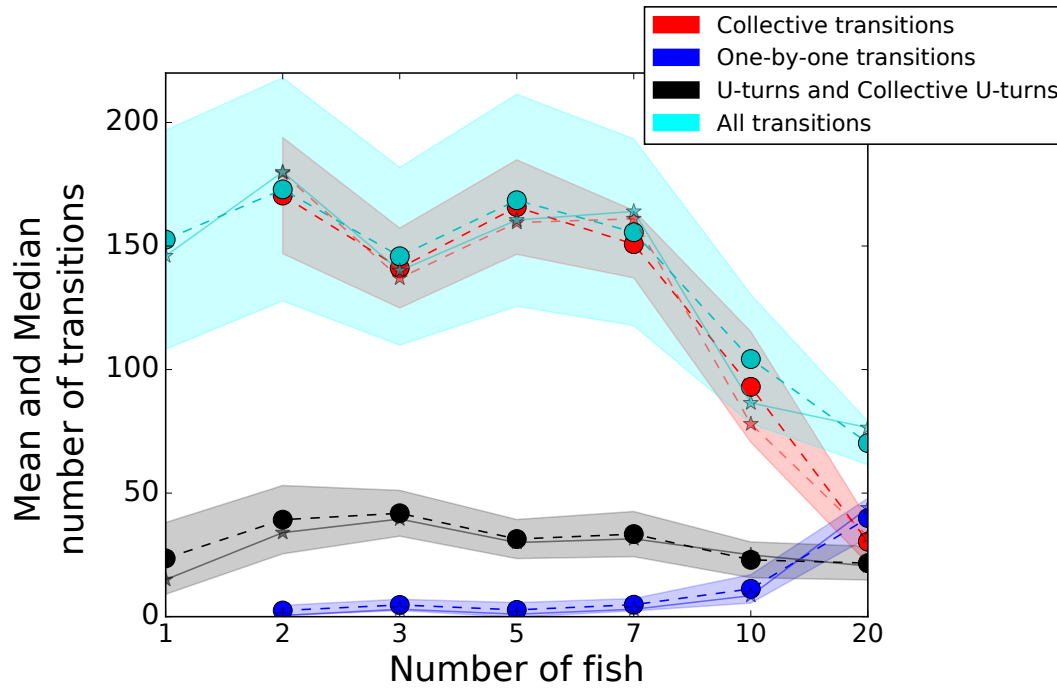


FIGURE 6.3 – **Mean and median number of transitions for different group sizes.** The red curve shows *Collective transitions*, the blue curve shows *One-by-one transitions*, the black curve represents the *Collective U-turns* and the magenta (*All transitions*) is the sum of *Collective transitions* and *One-by-one transitions*. The dots show the means and the stars the medians. *One-by-one transitions* occur when the fish transit one by one from one room to the other. *Collective transitions* appear when the group transit between both rooms through the corridor. *Collective U-turns* occur when the group go back to the previous room. The dashed lines facilitate the lecture. The figure shows that increasing the group densities makes the number of *Collective U-turns* and *Collective transitions* decrease and the number of *One-by-one transitions* increase. Each point shows the median of 12 values.

table of the rank of exit for all zebrafish from both rooms (without distinction) with the rank of the distances of all zebrafish to the initiator. These results correspond to 12 replicates of groups of 5 and 10 zebrafish. The initiator has a rank of exit and a rank of distances of 1. For example, in (A) the probability that the first fish to follow the initiator (rank 2) was also the closest fish of the initiator when it exited the room is 0.82. Figure 6.21 and S6.22 of the appendix show a more detailed version of the Figure 6.4 for 3, 5, 7 and 10 individuals. In Figure 6.5, we plot for 3, 5, 7 and 10 zebrafish the values of the probability of equal ranking between the exit and the distances with the initiator (i.e. the diagonal of the previous plots – Figure 6.4) for different time-lag before the exit of the initiator. In particular, we computed the ranking of the distance from the initiator at 1 to 5 seconds before the exit of the initiator. First, these measures show that the further from the time of the initiation the lower the probability of equal ranking. This assessment is valid for every group densities. Second, we see that the probability of equal ranking is often higher for the first and for

the last ranked fish even few seconds before the initiation (around 2 seconds before the initiation). In Figure 6.6, we use the Kendall rank correlation coefficient to see if the rank of exit and the rank of distances with the initiator are dependent (close to 1) or not (close to 0) through the time. For every group densities, we show an increase of the Kendall rank correlation coefficient when closer to the initiation. For 3 zebrafish, the time series shows that from 4 seconds before the initiation the Kendall rank correlation coefficient fully increases from 0.11 to 0.79 (at $T = t = 0$ s). For 5 zebrafish, it increases from 0.06 (at $T = t - 4$ s) to 0.75 (at $T = t = 0$ S), for 7 zebrafish, it increases from 0.10 to 0.70 and for 10 zebrafish, it increases from 0.08 to 0.58. These results show that for all group densities, the closer to the initiation the higher the correlation between the rank of exit and the rank of the distances with the initiator.

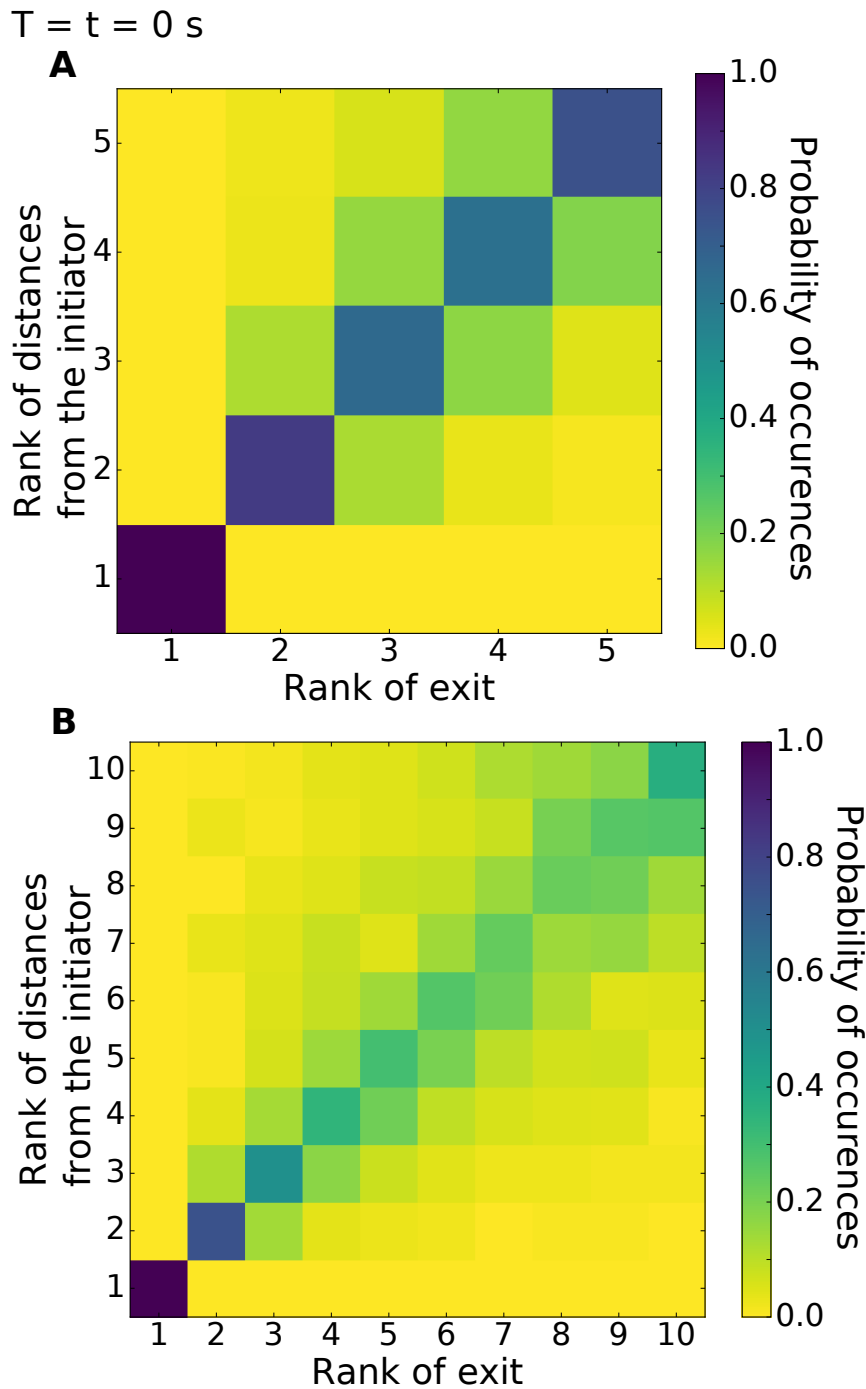


FIGURE 6.4 – **Probability of occurrence of the rank of exit with the rank of distance from the initiator** for population sizes of 5 zebrafish (left column) and 10 zebrafish (right column). We counted $N = 1456$ exits for 12 replicates with 5 zebrafish and $N = 277$ for 12 replicates with 10 zebrafish. (A) and (B) show the map at the time when the initiator leave the room. As an example, in (A) the probability of occurrence where the second fish leaves the room and has the shortest distance from the initiator is 0.82. This probability decreases to 0.12 for fish with rank of 2 for exit and rank of 3 for distances (the second closest distance from the initiator).

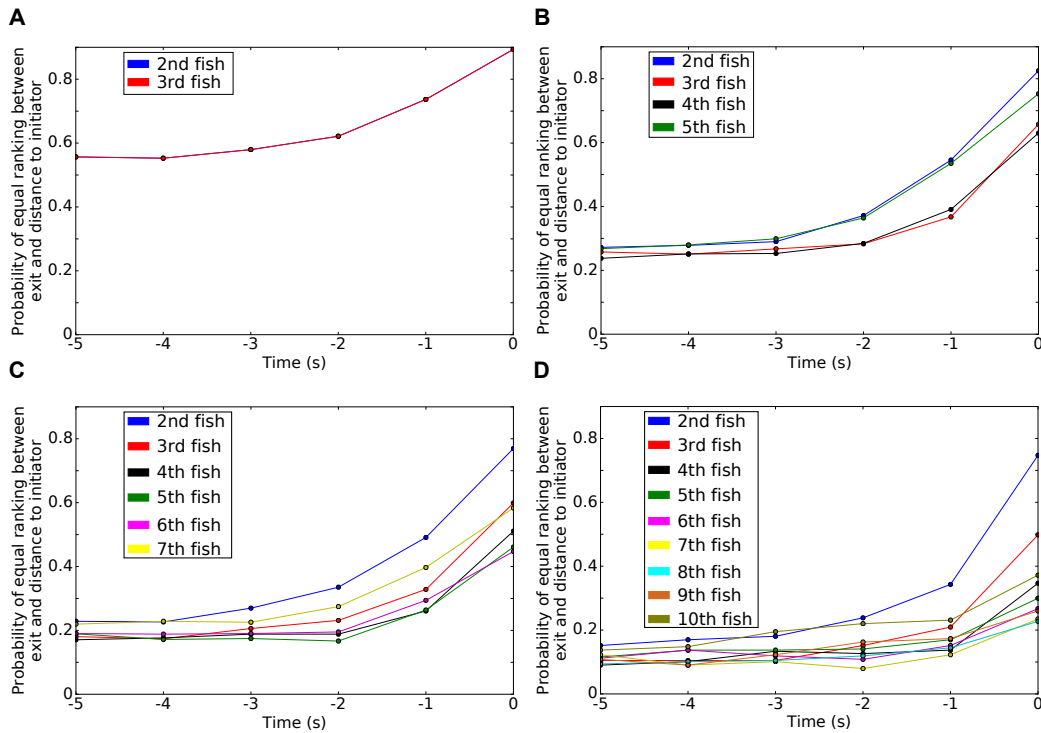


FIGURE 6.5 – Time series of the probability of equal ranking between the rank of exit and the rank of distances from the initiator for groups of (A) 3 zebrafish, (B) 5 zebrafish, (C) 7 zebrafish and (D) 10 zebrafish. This figure is related to the results shown in Figure 6.4 (the diagonal). We plot a time series of the 5 seconds before the initiation. We show that the probability increases strongly 2 seconds before the initiation. We see also that this probability is the highest for the first ranked fish and higher for the 3 first ranked fish and for the last ranked fish. This behaviour is also valid even few seconds before the initiation.

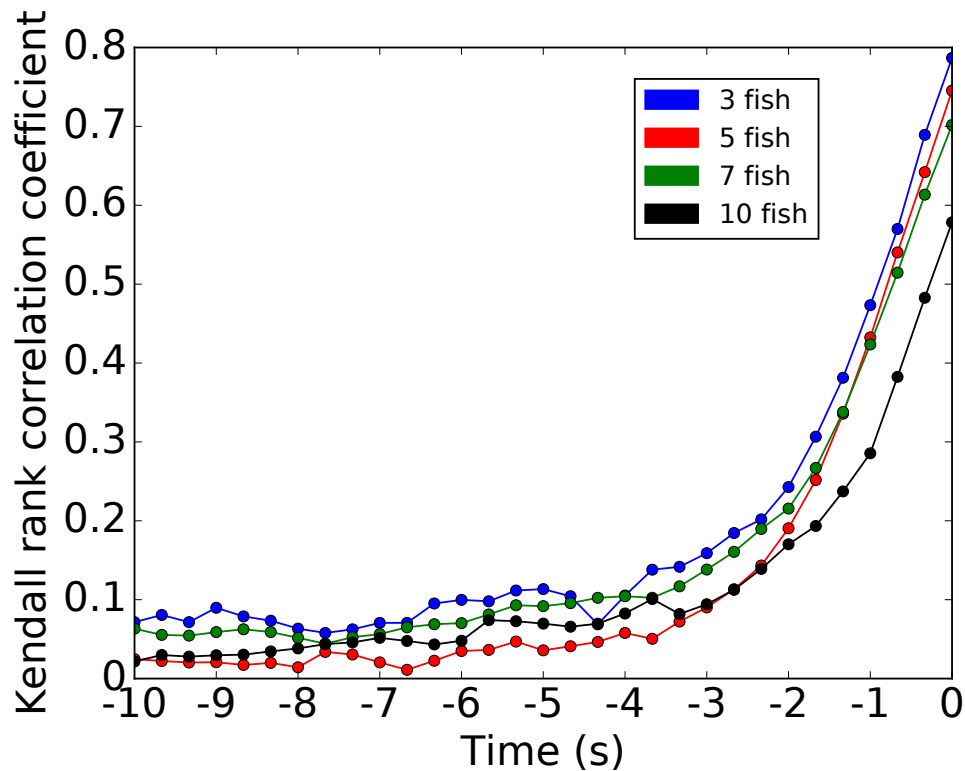


FIGURE 6.6 – **Time series of the Kendall rank correlation coefficient** calculated on the results of the Figures S6.21 and S6.22. It has been calculated every 1/3 second starting 10 seconds before the initiation. The Kendall rank correlation coefficient is a measure of ordinal association between two measured quantities. It goes to 0 when the two quantities are independent and goes to 1 if they are correlated. For example with 5 zebrafish, the time series shows that from 4 seconds before the initiation the Kendall rank increases from 0.06 to 0.75 (at $T = t = 0$ s). Whatever the size of the groups, we conclude that the closer to the initiation the higher the correlation between the rank of exit and the rank of the distances with the initiator.

6.5 Discussion

We studied the impact of the group density (1, 2, 3, 5, 7, 10 or 20 individuals) on the collective motion and the collective departure between two environmental patches in adult AB zebrafish. We show that the individual speed of the zebrafish varies according to the areas in which they are swimming and their group density. The zebrafish move faster in the corridor and have similar lower speeds in both rooms (Figure 6.15 of the appendix). The surface of the corridor is the third of a room and it constraints the direction the fish have to follow. We have shown that zebrafish are known to swim along the walls of the experimental tank [Collignon et collab. \[2016\]](#); [Séguret et collab. \[2016\]](#) thus showing a strong thigmotaxis. In the corridor, that can be compared to a tunnel, canalised by the walls of the corridor, the zebrafish increase their individual speeds to make the transit from one room to the other. In both rooms the means and the medians of the individual speeds are at their highest levels for groups of 3 zebrafish and the maximum of the means and the medians of the individual speeds is reached for group density of 5 fish in the corridor. In parallel, in each area these means and medians are at their lowest levels for the smallest and the biggest group densities : 1 and 10 zebrafish. Hence, in both rooms and in the corridor respectively, we have seen that from 1 to 3 individuals and from 1 to 5 individuals the individual speeds increase, when from 3 to 10 individuals and from 5 to 10 individuals, the individual speeds decrease. We showed also that the distances travelled by the zebrafish are related to the density of the group (Figure 6.14 of the appendix). Groups of 2 to 7 zebrafish travelled the longer distances (with a declining trend) and fish alone and groups of 10 zebrafish travelled the shorter distances.

First, our results confirm that the behaviour of a zebrafish alone differs significantly from the behaviour of zebrafish in groups. Isolated zebrafish travel a shorter distance and at a lower speed than zebrafish in groups. This can be the result of the stress generated by being isolated in a new environment. The stress level has been studied and [Egan et collab. \[2009\]](#) shows that some anxiolytics (fluoxetine and ethanol, that reduce stress level) will increase the speed and/or the travelled distances of zebrafish alone in a tank. Second, zebrafish swim faster in smaller group densities and their speeds decrease for bigger group densities. We observe the same trend for the travelled distances. These results may suggest a congestion effect where obstruction can affect their individual speeds and hence their travelled distances during the experimentation time [Chowdhury et collab. \[2005\]](#). Such effect has already been reported for example in the ant species *Atta cephalotes* : crowded conditions on the trail network make the velocity decrease [Burd et Aranwela \[2003\]](#). Herbert-Read et al. present another explanation for the changes of the motions where each fish (*Gambusia holbrooki*) conforms to the group behaviour through the interaction rules between the individuals and the decisions of each individual to follow or copy

their neighbour movements [Herbert-Read et collab. \[2013\]](#). Although this case seems to be extreme, [Burns et collab. \[2012\]](#); [Magnhagen et Bunnefeld \[2009\]](#); [Nakayama et collab. \[2012b\]](#) have shown that fish from different species (*Perca fluviatilis*, *Gasterosteus aculeatus*) and *Gambusia holbrooki* can maintain particular individual behavioural traits in a social context. These changes in behaviours are found in other animal species such as birds (*Erythrura gouldiae*) that adjust their behaviour according to the personality of their partners [King et collab. \[2015\]](#).

By analysing the distances between all pairs within a group we show that the larger the group the higher the medians of the distances between all respective pairs of zebrafish (Figures [6.1](#) and [6.11](#), [6.12](#) and [6.13](#) of the appendix). In parallel (Figure [6.16](#) of the appendix), if we focus on the neighbour distances, by increasing the density of the group (2 to 5 individuals) the median of the average neighbour distances decreases from 0.08m to 0.04m and stabilize around this value for groups of 7, 10 and 20 zebrafish. The combination of these results shows that there is a clear effect of the density on the cohesion of the group; an effect that we already have shown in [Séguret et collab. \[2016\]](#) where the bigger the group the higher the cohesion of the whole group.

It seems that there are preferential interactions between zebrafish (Figure [6.11](#), [6.12](#) and [6.13](#) of the appendix) and increasing the density of the group will affect these interactions (Figure [6.1](#)): respective pairs are less cohesive in larger groups. Preferential interactions have been evidenced in other species: Briard et al. [Briard et collab. \[2015\]](#) show affinities, hierarchy and pairs interactions in a group of domestic horses, Sueur et al. and King et al. [King et collab. \[2011\]](#); [Sueur et Petit \[2008\]](#); [Sueur et collab. \[2009\]](#) show that the affinity between individuals (*Macaca mulatta*, *Macaca tonkeana* and *Papio ursinus*) play a role in the collective movements. We propose two hypotheses that could explain the change of the interactions between pairs of zebrafish when changing the density of the group. On the one hand, in groups larger than 2, each zebrafish has to choose the preferred partners, between all other fish. In larger groups there are more individual choices and more preference tests. On the other hand, the patchy environment may break pair interactions and may force the emergence of new pairs. These two hypotheses could explain the dynamics of the pair interactions observed during the experiments.

The fish are detected 70% of the time in the rooms (Figure [6.19](#)). On average, they spend about 10 seconds in a room (Figure [6.18](#)) then transit the the other one through the corridor (about 4 seconds on average) and then come back. They oscillate between the rooms. In a previous study we showed that zebrafish also transit and oscillate between landmarks in an open environment [Séguret et collab. \[2016\]](#). Figure [9.4](#) shows that most

of the transitions are collective. Compared with Figure 6.2 it shows that the whole group swim together in both rooms. This observation is strengthened by the very rare number of "One-by-one" transitions between the rooms. However, groups of 10 and 20 zebrafish show sharp decreases in the number of collective transitions. This drop could be due to the topology of the set-up and congestion effects. Larger groups can split into smaller sub-groups (we can call this phenomenon fission). The threshold we imposed in the analysis of the collective transitions (below 70% of the whole group, the transitions were not taken into account) may reinforce this effect. This seems to be confirmed by the Figure 6.2 that shows a larger occurrence of fish distribution between both rooms for larger group density. Many studies have analysed the fusion-fission mechanisms occurring in groups of fish or mammals. Croft et collab. [2003]; Hoare et collab. [2000]; Krause et Ruxton [2002] show that these mechanisms are frequent in the wild and generate body length assortment within groups of fish (*Fundulus diaphanus*, *Notemigonus crysoleucas*, *Catostomus commersonii*, *Poecilia reticulata*). Sueur et al. Sueur et collab. [2011b] show that fission-fusion mechanisms participate in the information transfer between sub-groups and the group of *Myotis bechsteinii*.

In the corridor, we observe few u-turns. The zebrafish swimming preferentially along the walls and a canalisation effect of the corridor may explain this observation. The zebrafish also show higher speeds in the corridor. As expected, the corridor connecting the two patches is used as a mere transit area.

We show that the organisation of the group appears during collective departure and is related to the distances between the initiator of the exit from the room and the other fish. Ward *et al.* has shown that the first fish (of a group of 5 *Dascyllus aruanus*) to follow the initiator is generally (rank = 2 : 53% of the trials over 2 trials for each 15 groups of fish) the nearest neighbour of the initiator and that the frequency of equality between the rank of exit and the rank of the distances from the initiator decreases, with these results rank = 3 : 27% and 33%, rank = 4 : 20% and 7% then rank = 5 : 0% and 7%) Ward et collab. [2013]. We tested 4 group densities (3, 5, 7 and 10 zebrafish) and show similar results especially on the decreasing trend of the probability when focusing on the next ranked fish Figures S6.22, S6.21 of the appendix and Figure 6.5. However, we observe an extremely high probability of equal ranking for the first fish that follows the initiator (rank = 2 : 75% to 90%), high probabilities of equal ranking for the second and the last fish that follow the initiator (rank = 3 : 50% to 65% and rank = last fish : 38% to 75%) and show that the probabilities of equal ranking for the other fish are quite similar to each others. The rank of exit and the rank of the distances from the initiator are strongly correlated at the moment of the exit ($T = 0s$, Figure 6.6), from 60% to 80%. Hence, it seems that the organisation of the zebrafish groups (2nd, 3rd and last ranked fish) during the collective

departures is topological. Other studies about the organisations of collective departures show a joining process for *Equus ferus caballus* that is related to affinities and hierarchical rank Briard *et collab.* [2015]. Rosenthal *et al.* show that, in groups of *Notemigonus crysoleucas*, the initiator is the closest fish from the group boundary in 27% of the cases and the first responder is the closest fish from the group boundary in 19% of the cases Rosenthal *et collab.* [2015]. Moreover during the initiation, when fish leave the rooms, our results suggest the idea of cascades of behavioural changes already developed by Rosenthal *et al.* Rosenthal *et collab.* [2015] : the initiator drags another fish along that drags another one, etc.

This organisation appears a few seconds before the fish leave a room to transit to the other one. Two seconds before the initiation, the group show a structure that prepares for the exit (Figure 6.5). The Kendall rank correlation coefficient confirmed the idea of the organisation as it reaches 18% to 25% two seconds before the departure and 30% to 50% one second before the departure (Figure 6.6). In the literature we found other cases of initiations : Leblond *et Reeb*s [2006]; Pillot *et collab.* [2010] have shown that a three-spined stickleback *Gasterosteus aculeatus* or a sheep *Ovis aries* alone moving away from the herd can initiate a collective departure, Byrne *et collab.* [1990] have noticed a large variety of initiations for groups of mountain baboons *Papio ursinus* where the initiator can be joined by the group immediately or Leca *et collab.* [2003]; Petit *et collab.* [2009] have observed for white-headed capuchins *Cebus capucinus* a synchronization of their behaviours and a minimum proportion of the whole group is able to launch a collective departure.

In conclusion, this study shows that the density of the group and the structure of the environment affect the motion of each individual in the groups and the group cohesion. The analysis of the dynamics shows that the zebrafish oscillate mainly in groups between the two patch in the environment and that the majority of the departures are collective. During the collective departures, we observe that an intra-group organisation appears prior to the transition. Increasing the group density makes this organisation less predictable. Finally, we noticed that a few seconds before the collective departures the groups has a particular spatial organisation.

6.6 Methods

Fish and housing

We bred 600 AB strain laboratory wild-type zebrafish (*Danio rerio*) up to the adult stage and raised them under the same conditions in tanks of 3.5L by groups of 20 fish in a ze-

brafish aquatic housing system (ZebTEC rack from Tecniplast) that controls water quality and renew 10% of water in the system every hour. Zebrafish descended from AB zebrafish from different research institutes in Paris (Institut Curie and Institut du Cerveau et de la Moelle Épineuse). AB zebrafish show zebra skin patterns and have short tail and fins. They measured in mean = 3.0 cm \pm 0.36 cm, median = 2.9 cm long. All zebrafish used during the experiments were adults from 7 to 8 months of age. We kept fish under laboratory conditions : 27°C, 500 μ S salinity with a 10 :14 day :night light cycle, pH is maintained at 7.5 and nitrites (NO²⁻) are below 0.3 mg/L. Zebrafish are fed two times a day (Special Diets Services SDS-400 Scientific Fish Food).

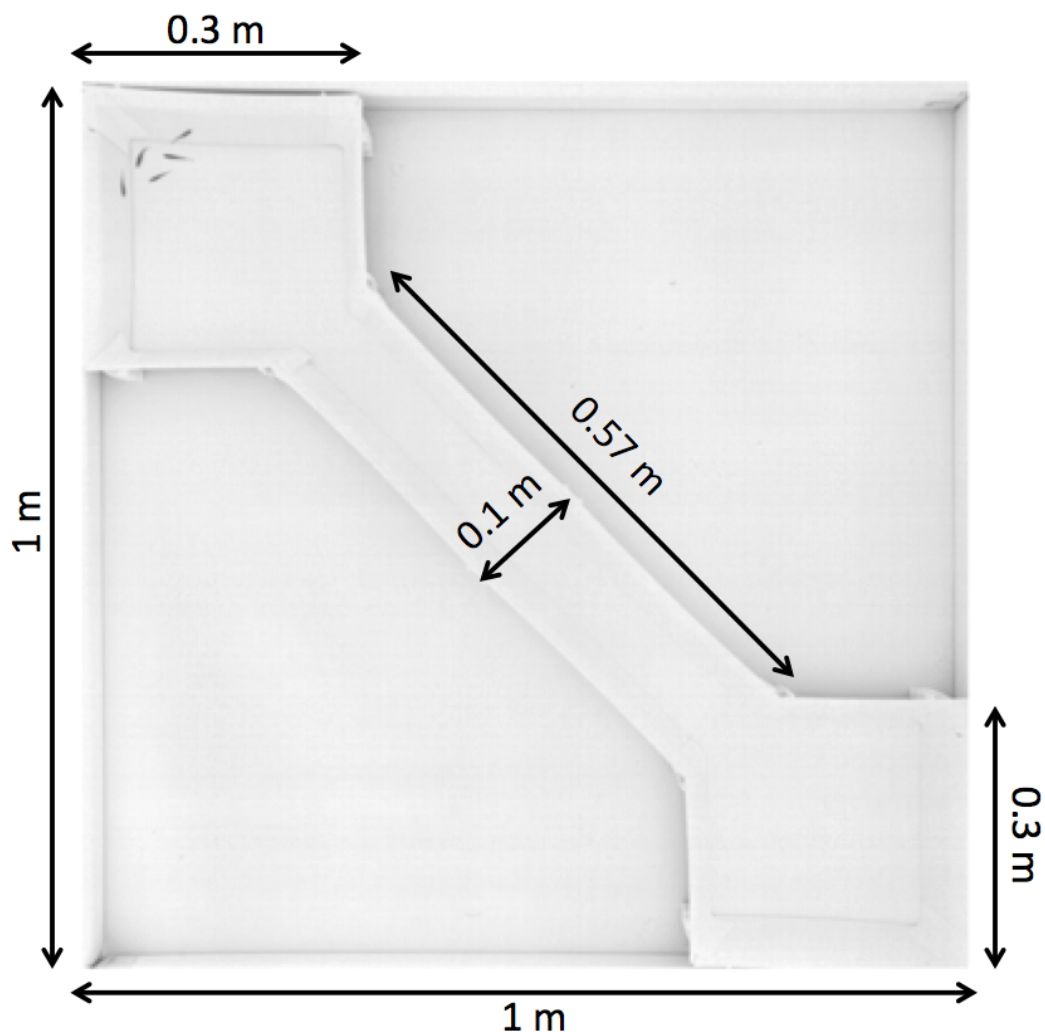


FIGURE 6.7 – **Experimental setup.** A tank of 1 m x 1 m is divided into three areas : two rooms (0.3 m x 0.3 m) connected by a corridor (0.57 m x 0.1 m). The water column has a height of 6 cm. The luminosity is ensured by 4 LED lamps of 33W (LP-500U) placed on corners of the tank and directed towards the walls to provide indirect lighting. The whole setup is confined in a 2 m x 2 m x 2.35 m experimental chamber surrounded by white sheets to isolate the experiments and to homogenise luminosity.

Experimental setup

The experimental tank consisted in a 1.2 m x 1.2 m tank confined in a 2 m x 2 m x 2.35 m experimental area surrounded by white sheets, in order to isolate the experiments and homogenise luminosity. A white opaque perspex frame (1 m x 1 m x 0.15 m - interior measures) is placed in the center of the tank. This frame helped us to position the two rooms and the corridor. The squared rooms (0.3 m x 0.3 m) and the corridor (0.57 m x 0.1 m) have been designed on Computer-Aided Design (CAD) software and cut out from Poly(methyl methacrylate) (PMMA) plates of 0.003 m thickness. Each wall are tilted, (20° from the vertical) to the outside with a vertical height of 0.14 m, to avoid the presence of blind zones for the camera placed at the vertical of the tank. The water column had a height of 6 cm, the water pH is maintained at 7.5 and Nitrites (NO²⁻) are below 0.3 mg/L. The experiments are recorded by a high resolution camera (2048 px x 2048 px, Basler Scout acA2040-25gm) placed above the experimental tank and recording at 15 fps (frame per second). The luminosity is ensured by 4 LED lamps of 33W (LED LP-500U, colour temperature : 5500 K - 6000 K) placed on each corner of the tank, above the aquarium and directed towards the walls to provide indirect lightning.

Experimental procedure

We recorded the behaviour of zebrafish swimming in the setup during one hour and did 12 replicates with groups of 1, 2, 3, 5, 7, 10 and 20 zebrafish. Every six replicates the setup is rotated by 90° to prevent potential environmental bias (noise, light, vibrations, ...). Before each replicate, the starting chamber, from which the fish are released, is chosen randomly. We called the starting chamber *Room 1*. Then, the fish are placed with a hand net in a cylindrical arena (20 cm diameter) made of Plexiglas in the centre the selected rooms. Following a five minutes acclimatisation period, this cylinder is removed and the fish are free to swim in the setup. The fish are randomly selected regardless of their sex and each fish is never tested twice to prevent any form of learning.

Tracking & data analysis

Today, the studies on animal collective behaviours use methodologies based on massive data gathering, for exemple for flies (*Drosophila melanogaster*) [Branson et collab. \[2009\]](#); [Dankert et collab. \[2009\]](#), birds (*Sturnus vulgaris*) [Ballerini et collab. \[2008\]](#); [Miller et Gerlai \[2007, 2011\]](#), fish (*Notemigonus crysoleucas*) [Strandburg-Peshkin et collab. \[2013\]](#). Our experiments are tracked in real-time ("on-line") by a custom made tracking system based on blob detection. Each replicate except experiments with 20 zebrafish is also tracked by post-processing ("off-line") with the idTracker software to identify each fish and their positions [Pérez-Escudero et collab. \[2014\]](#). Each replicate consisted of 54000

positions (for one zebrafish) to 1080000 positions (for 20 zebrafish). The idTracker software is not used for groups of 20 fish due to higher number of errors and too long computing time. For example, for a one hour video with 2 fish idTracker gives the results after 6 hours of processing and for a one hour video with 10 fish it lasts a week to do the tracking (with a Dell Percision T5600, Processor : Two Intel Xeon Processor E5-2630 (Six Core, 2.30GHz Turbo, 15MB, 7.2 GT/s), Memory : 32GB (4x8GB) 1600MHz DDR3 ECC RDIMM).

Since idTracker solved collisions with accuracy [Pérez-Escudero et collab. \[2014\]](#) we calculated individual measures and characterised the aggregation level of the group. We also calculated the distances between each pair of zebrafish respectively, the travelled distances of each individual and their speeds. The calculation of the speed has been done with a step of a third of a second in sort of preventing the bias due to the tracking efficiency of idTracker that does not reach 100% (see Table 6.1 of the appendix).

The Figure 6.2 has been obtained following this process : At each time step with at least one fish detected in a room, we analysed the repartition of the group among the rooms by computing the proportion of fish present in room 1 = $R_1 / (R_1 + R_2)$ with R_1 and R_2 the number of fish in the respective room number.

When all fish were present in the same room, we identified which fish initiates the exit from the room, established a ranking of exit for all the fish and calculated the distances between all zebrafish to the initiator to establish a ranking of distances. Finally, we confronted these ranks and count the number of occurrences for each ranking case. We checked the results for different time steps before the initiation. The idea was to highlight a correlation between the spatial sorting and the ranks of exit and also a possible prediction of ranking of exit.

The Kendall rank correlation coefficient [Kendall \[1938\]](#), τ , is a measure of ordinal association between two measured quantities. It goes to 0 when the two quantities are independent and to 1 if they are correlated. It is compute by :

$$\tau = \frac{\text{number of concordant pairs} - \text{number of discordant pairs}}{\text{number of concordant pairs} + \text{number of discordant pairs}}$$
 We use the Kendall rank correlation coefficient to see if the rank of exit and the rank of distances with the initiator are dependant or not through the time.

Finally, we looked at majority events defined as the presence of more than 70% of the zebrafish in one of the three areas of the setup, either in the room 1 or in the room 2 or in the corridor. To compute their numbers, we averaged the number of fish over the 15 frames of every second. This operation guaranties that a majority event is ended by the departure of a fish and not by an error of detection during one frame by the tracking system. We then computed the durations of each of those events and counted the transitions from a room to the other one and sort them. All scripts were coded in Python using scientific and statistic libraries (numpy, pylab, scilab and matplotlib).

Statistics

All scripts were coded in Matlab and Python using statistic libraries (numpy, pylab, scilab and matplotlib). For the Figure 6.15 we report the number of values of the speeds on the Table S?? of the appendix. For the Figures 6.15, 6.1 and 6.3 we tested the distributions using Kruskal-Wallis tests completed by a post-hoc test : Tukey's honest significant difference criterion.

6.7 Supplementary information and figures

Supplementary figures of "Loose social organisation of AB strain zebrafish groups in a two patches environment".

6.7.1 From the individuals to the pair interactions

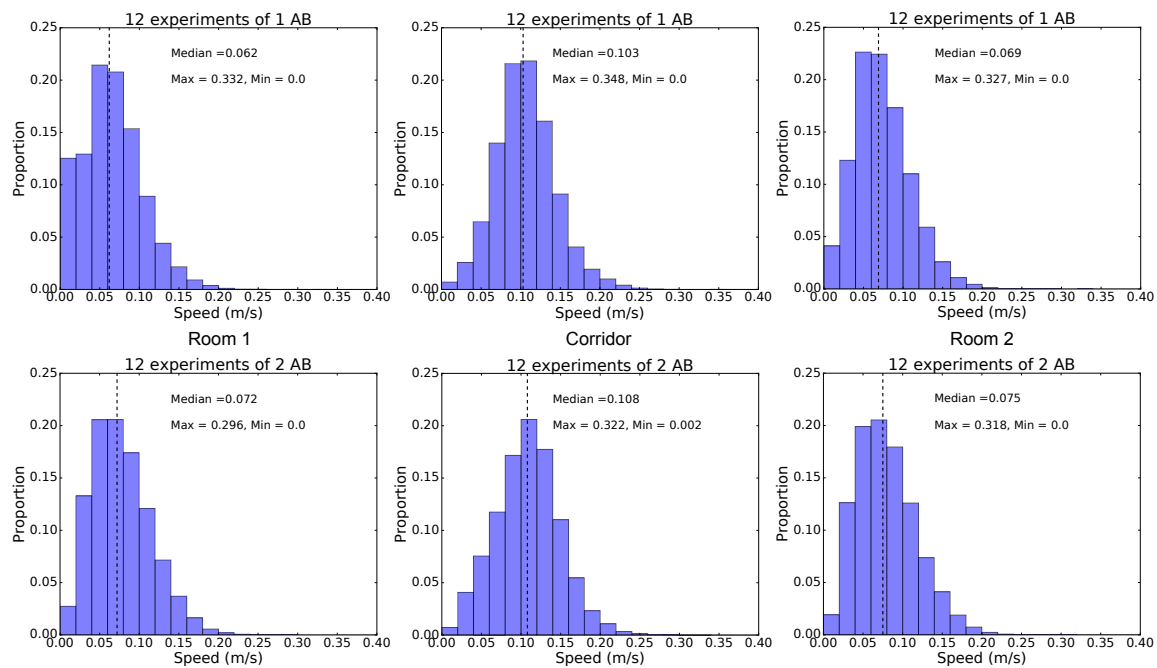


FIGURE 6.8 – Distribution of the individual speeds for an individual and a pair of AB zebrafish.

CHAPITRE 6. LOOSE SOCIAL ORGANISATION OF AB STRAIN ZEBRAFISH GROUPS IN A TWO-PATCH ENVIRONMENT

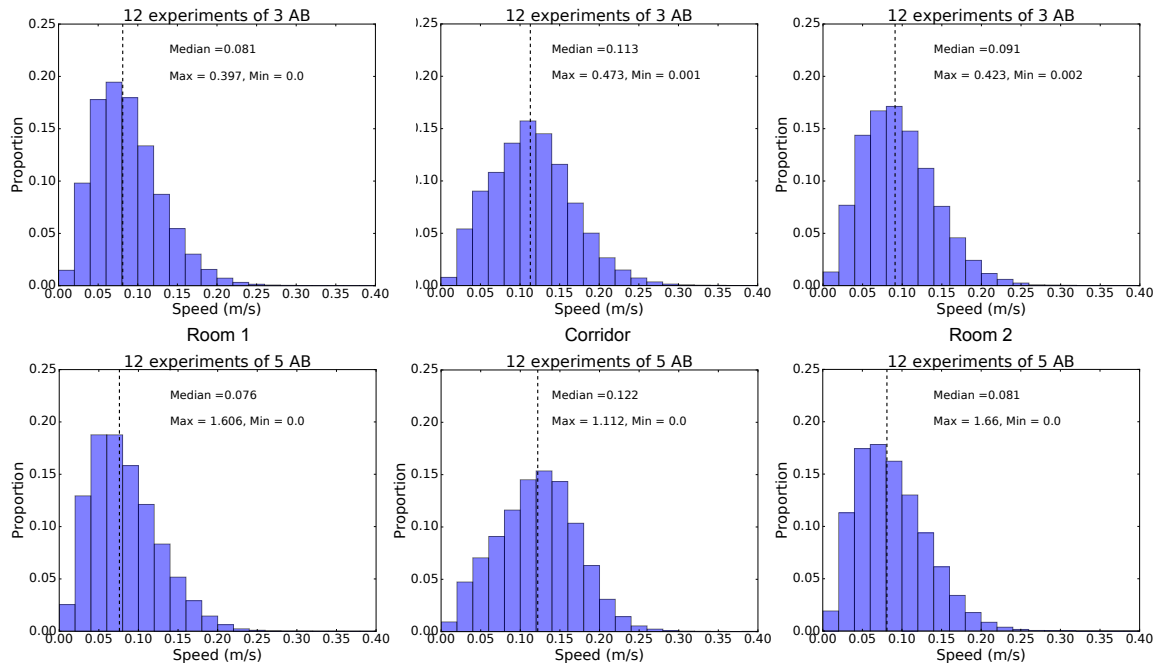


FIGURE 6.9 – Distribution of the individual speeds for two group sizes. Groups of 3 and 5 AB zebrafish.

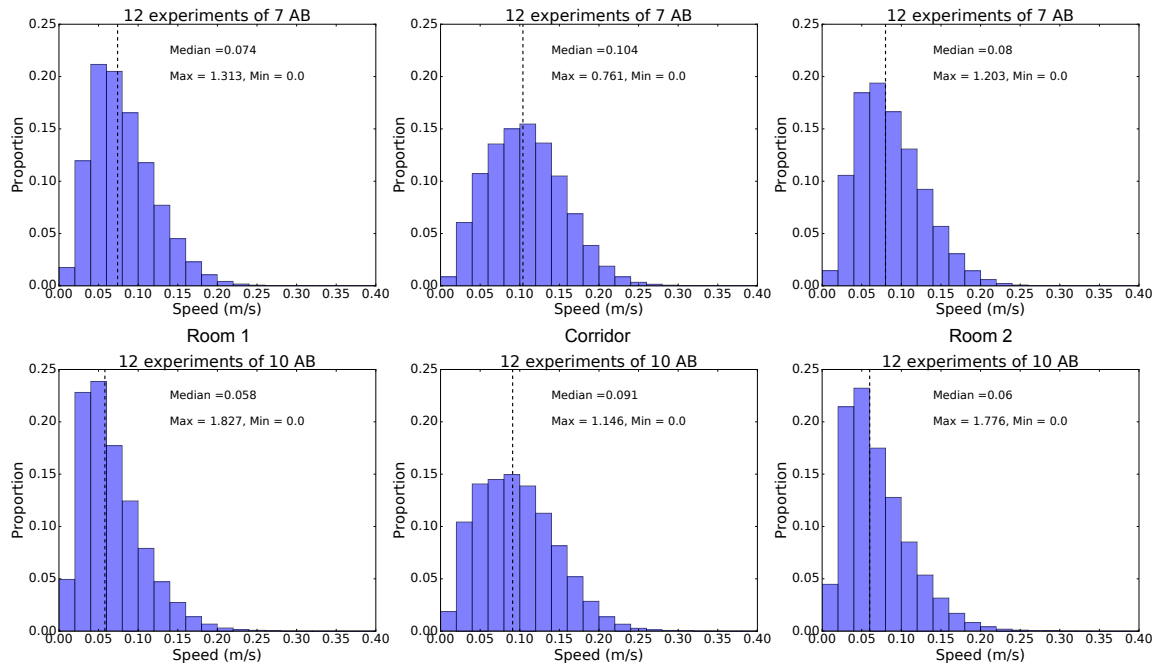


FIGURE 6.10 – Distribution of the individual speeds for two group sizes. Groups of 7 and 10 AB zebrafish.

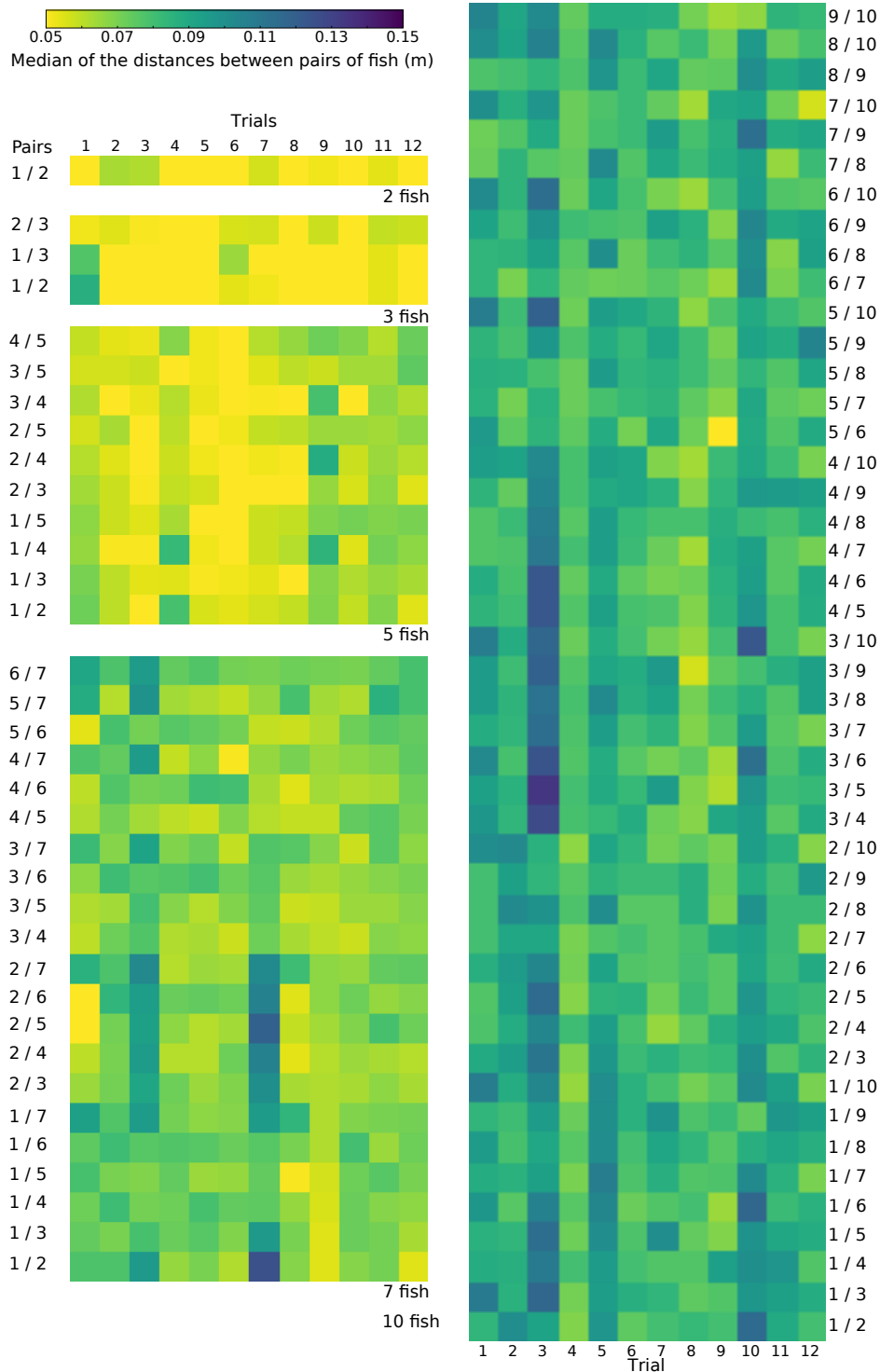


FIGURE 6.11 – Medians of the distances between all respective pairs of zebrafish per trial in the room 1 for 5 different group sizes. Each square corresponds to the median of the distances between the fish of one specific pair during a whole trial (out of 12 trials). When the colour of the square is yellow it means that the median of the distances between the fish is small (0.05m), when the colour is dark-blue it means that the median of the distances is larger (0.15m). For each area, we see a large distribution of the medians of the distances and their increase with the population size.

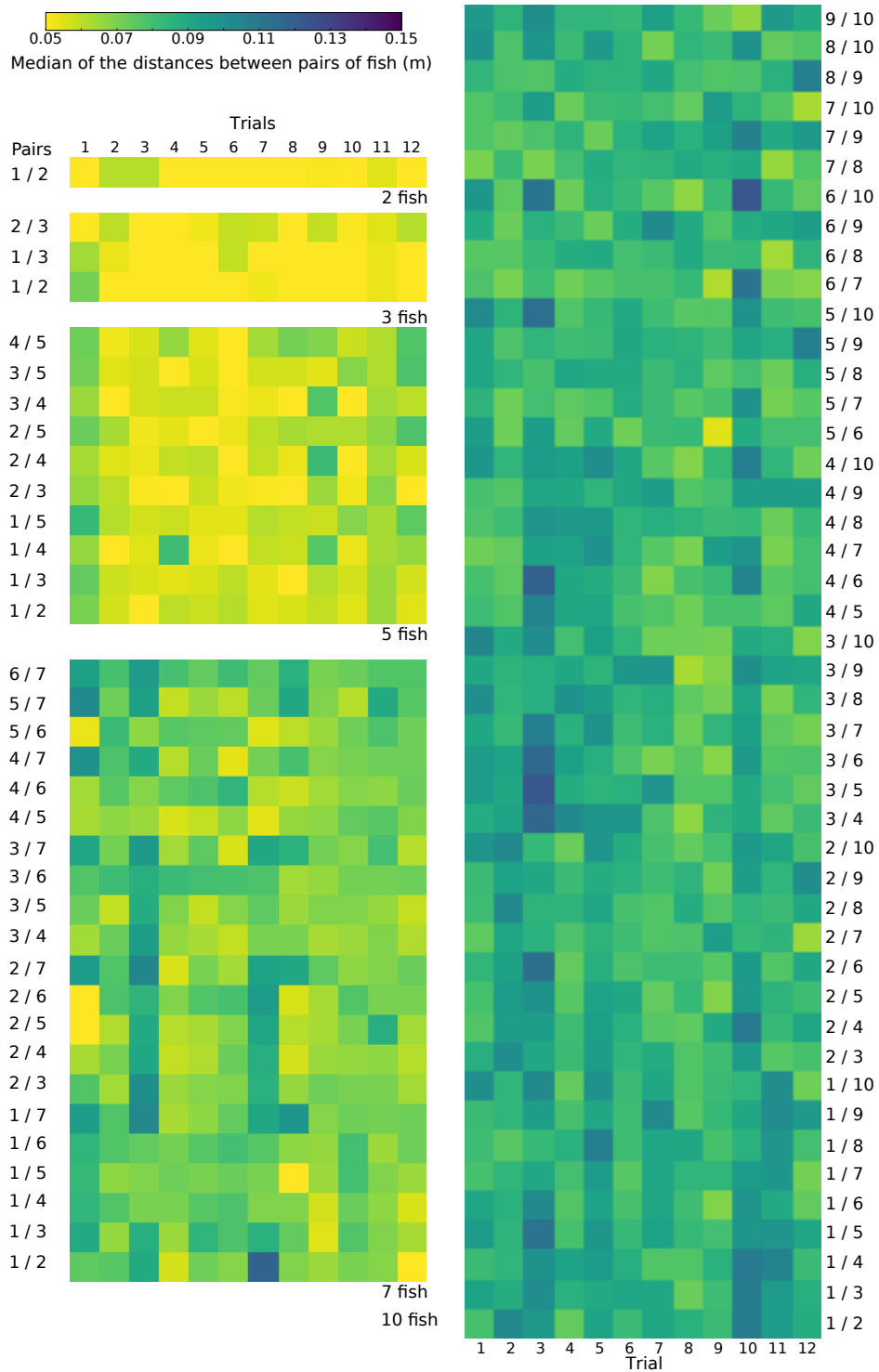


FIGURE 6.12 – Medians of the distances between all respective pairs of zebrafish per trial in the room 2 for 5 different group sizes.

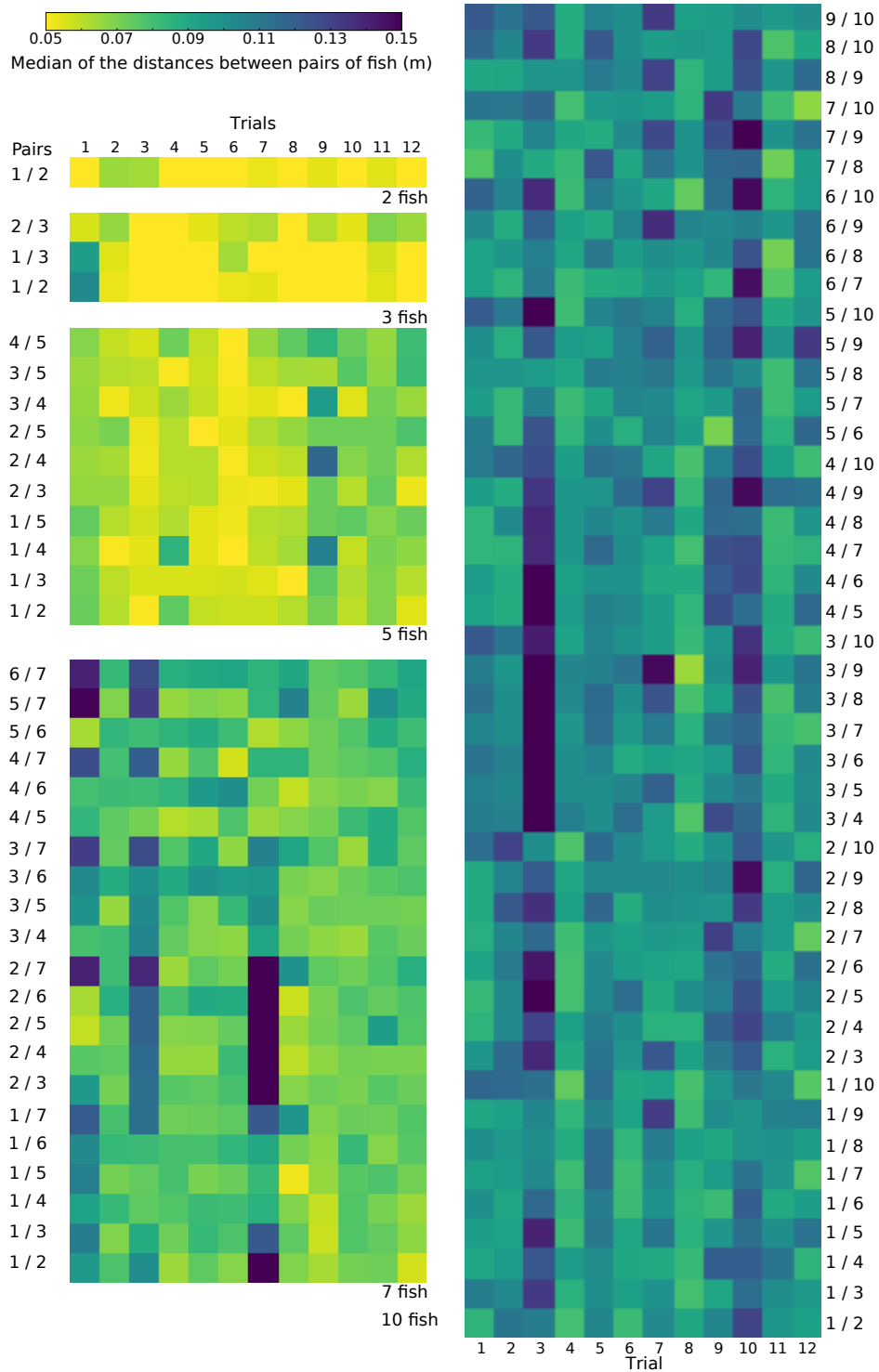


FIGURE 6.13 – Medians of the distances between all respective pairs of zebrafish per trial in the corridor for 5 different group sizes.

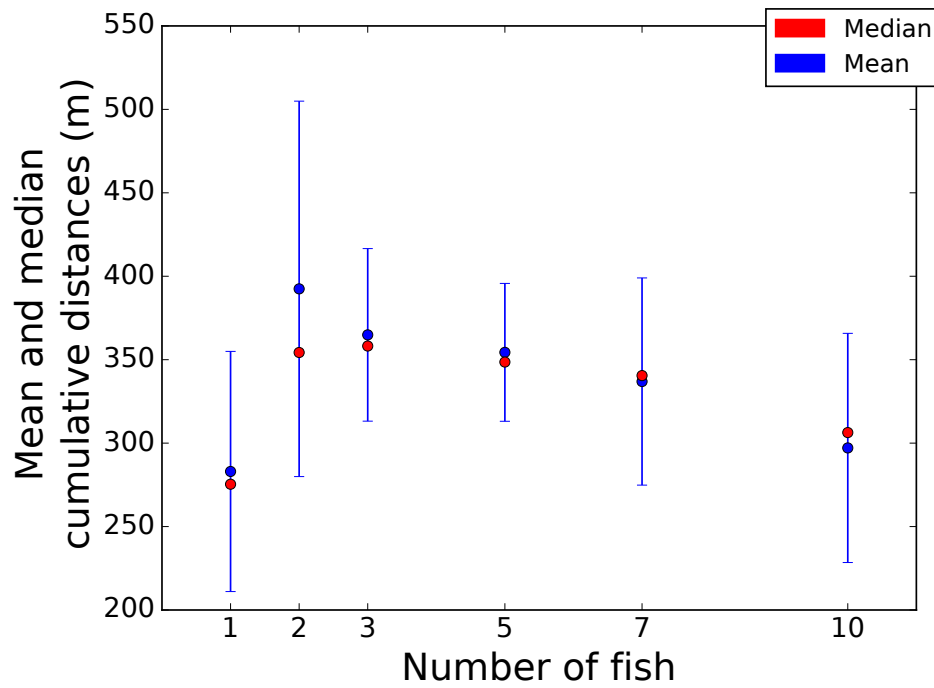


FIGURE 6.14 – **Mean and median cumulative travelled distances for different group densities.** The blue points represent the means, the red dot the medians. Small groups of zebrafish travel more than bigger groups and fish alone.

Figure 6.15 shows the means and the medians of the individual speeds of the fish measured during the entire experimental time (one hour) and according to their spatial location (in the corridor or in one of the two rooms). The fastest individuals are observed in groups of 5 fish in the corridor and 3 fish in both rooms. On the contrary, fish alone and groups of 10 individuals show the slowest mean and median speeds. Moreover in the corridor, between the group densities of 1 and 5 individuals, there is an increase of the mean and median speed. Then, for higher densities, the means and medians decrease. Likewise, in both rooms, for the group densities of 1 and 3, we observe an increase of the mean and the median of the speeds, then for bigger group sizes a drop. First, we compared, for each group density tested independently, the speed of the individuals according to their location (in the corridor, in room 1 or in room 2). For all the group densities, the speed of the individuals was significantly higher in the corridor than in the two rooms (for each group size : Kruskal-Wallis, $p < 0.001$, Tukey's honest significant difference criterion, $p < 0.001$ for corridor versus room 1 and $p < 0.001$ for corridor versus room 2). Indeed, the fish increase their swimming speed by approximately 3.5 cm/s in the corridor. They simply use the corridor to transit rapidly from room to the other. The difference between the speed measured in room 1 and room 2 was also significantly different for all the group densities (Tukey's honest significant difference criterion, $p < 0.001$ for room 1 versus room 2). Although in this case, the difference between the swimming speed was always lower than 1 cm/s. Secondly, we compared the speed of the individuals in similar areas but for different group densities. For each area (corridor, room 1 and room 2), the speed of the fish differs between all group densities (for each area : Kruskal-Wallis, $p < 0.001$, Tukey's honest significant difference criterion, $p < 0.001$ for all comparison) except in the corridor for groups of 1 and 7 fish. These first results show that both the group density and the location of the fish have an influence on their individual speed.

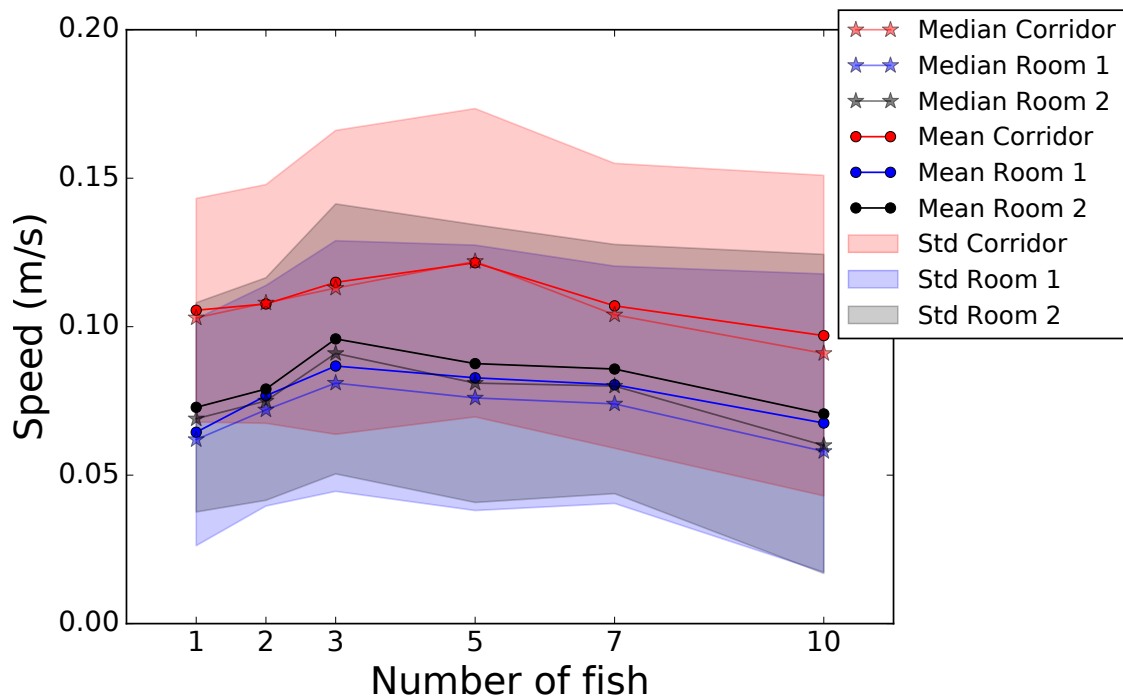


FIGURE 6.15 – **Mean and median of the individual speeds for different group densities.** The red dots represent the mean and the red stars the medians of the individual speed for all individuals in the corridor, the blue dots represent the mean and the blue stars the medians for the room 1 and the black dots represent the mean and the black stars the medians line for the room 2. The zebrafish move faster in the corridor. In rooms 1 and 2, their speeds are similar. Groups of 3 zebrafish show the highest speeds in both rooms and groups of 5 zebrafish the highest speeds in the corridor.

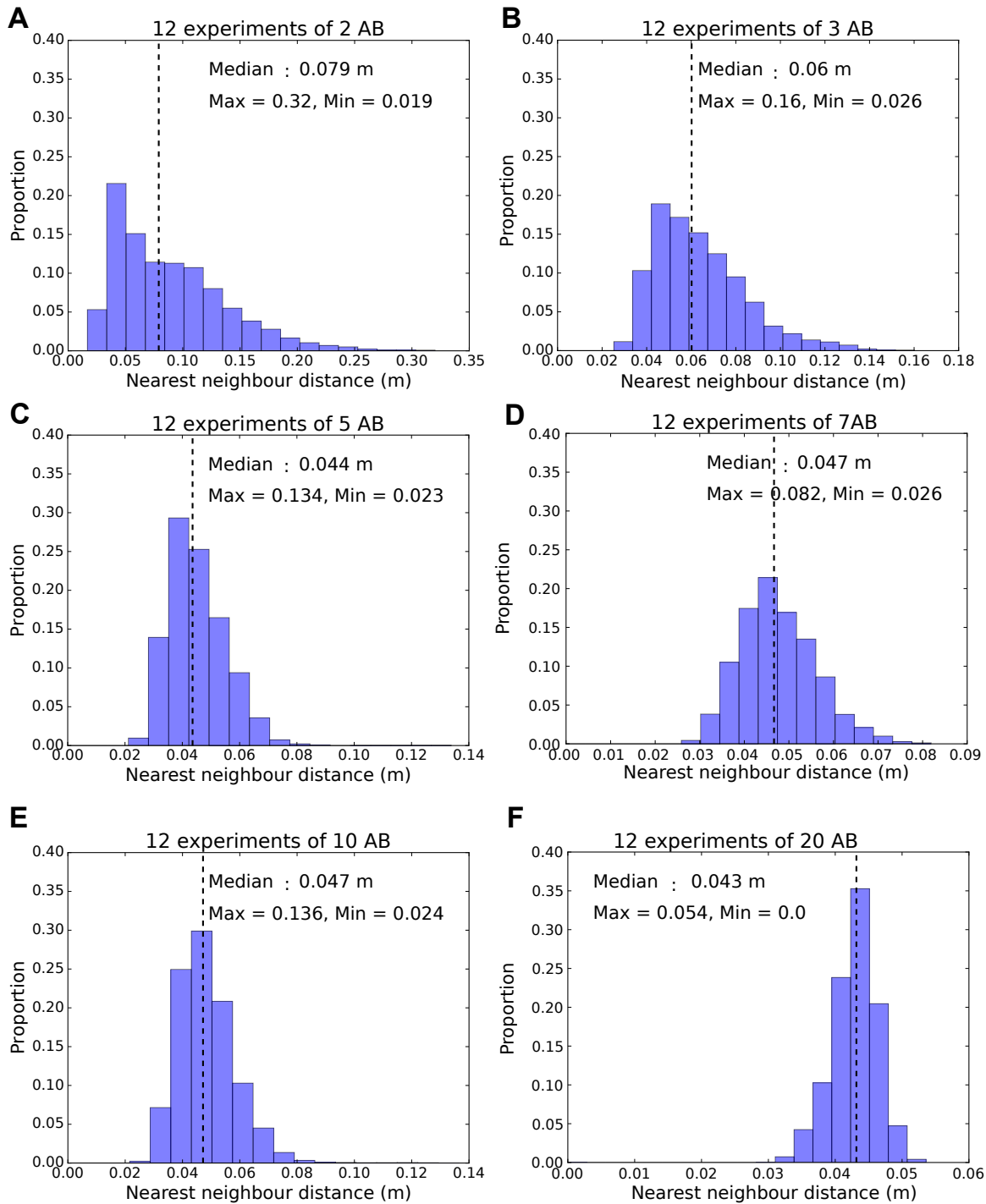


FIGURE 6.16 – **Distributions of the nearest neighbour distances.** Groups of (A) 2 AB zebrafish, (B) 3 AB zebrafish, (C) 5 AB zebrafish, (D) 7 AB zebrafish, (E) 10 AB zebrafish and (F) 20 AB zebrafish. The plots are based on 648012 distances for 12 replicates. The dashed lines represent the medians. The distributions show for groups of 5, 7, 10 and 20 zebrafish similar medians and a shift to higher median values for smaller groups : 2 and 3 zebrafish. The nearest neighbour distances refer to the shortest distances between all zebrafish at every time step. It is a measure of group cohesion. The interest of such analysis is to dismiss the effect of the geometry of the set-up and to focus only on the group bearing.

6.7.2 Oscillations and collective departures

To analyse the dynamics of the space occupancy in the set-up we computed the mean number of majority events and the mean durations and cumulative durations of occupancy by a majority of individuals within the three areas when a majority of the whole group is reached (Figure 6.17 and Figure 6.18). We define the majority as 70% of the individuals being present in the considered section of the set-up. On the Figure 6.17, we find more majority events in the corridor than in room 1 or room 2 except with groups of 20 zebrafish. Whatever the density of the group, we find almost the same number of majority events inside the rooms 1 and 2. Also, in all areas we see that for groups of 10 and 20 zebrafish the bigger the group the lower the number of majority events. The difference between the number of majority events in the corridor and in both rooms is relatively stable for groups of 1, 2, 3, 5 and 7 zebrafish but decreases when increasing the density of the groups (10 to 20 zebrafish). The mean number of majority events finally reaches almost the same value when 20 zebrafish are tested in the setup (room1 : 51,2; room 2 : 43.5; corridor : 41.7). Table S6.2 of the appendix (A) shows, for the 12 replicates of each group density, the standard deviations linked with the number of majority events (related to Figure 6.17). On the Figure 6.18, we see that the means of the durations of the majority in each area follow a similar trend in both rooms and are longer than in the corridor. Increasing the density of the group has almost no effect on the durations in the corridor when it has an impact in the rooms, where fish stay longer in majority if the group density increases. However, for 20 zebrafish, durations decrease in all areas. Table S6.2 (B) of the appendix shows the standard deviations related to the Figure 6.18.

Group size	1 fish	2 fish	3 fish	5 fish	7 fish	10 fish	20 fish
Mean tracking efficiency	*	*	*	*	*	*	
	100%	97%	98%	89%	94%	75%	94%

TABLEAU 6.1 – **Mean tracking efficiency.** The experiments are tracked by the idTracker program to find the individual identities and the positions of the fish Pérez-Escudero et collab. [2014].

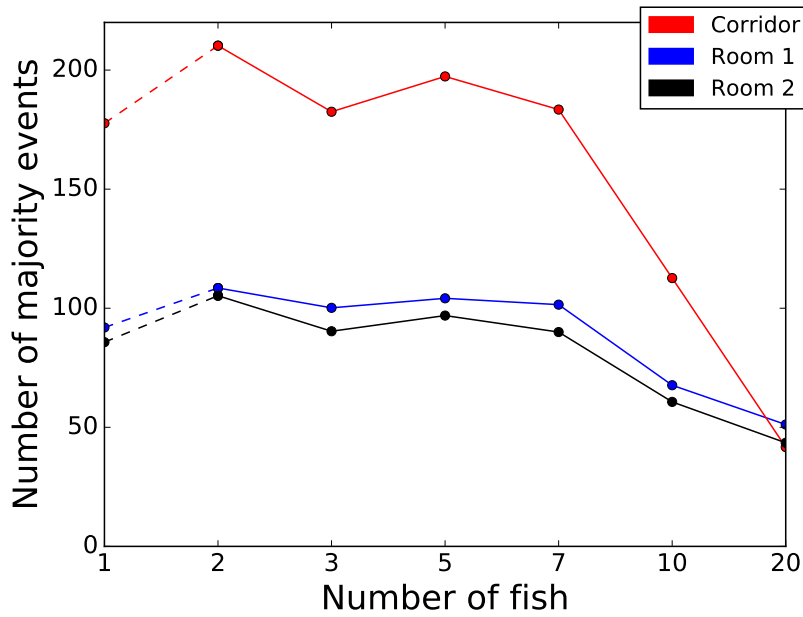


FIGURE 6.17 – Means of majority events with a majority of zebrafish in the three areas, for 7 group sizes for 12 replicates each. To calculate the majority events, we count every time a majority of fish is located in one of the three areas. The red line indicates the number of majority events within the corridor, the blue line shows the number of majority events within the room 1 and the black line in the room 2. The dashed lines distinguish the experiments with one fish from the experiments with groups of fish. For all group sizes except for 20 zebrafish, there are more majority events in the corridor. The majority events are also very similar between room 1 and room 2. The number of majority events is relatively stable for groups of 1, 2, 3, 5 and 7 zebrafish in all three areas.

(A) Majority events	1 fish	2 fish	3 fish	5 fish	7 fish	10 fish	20 fish
Std. corridor	62.5	42.4	35.7	41.3	33.3	49.4	19.2
Std. room 1	30.2	17.4	18.8	21.0	14.5	26.1	14.3
Std. room 2	33.0	28.0	19.8	21.3	19.8	24.6	15.8
(B) Durations (s)	1 fish	2 fish	3 fish	5 fish	7 fish	10 fish	20 fish
Std. corridor	1.73	1.94	2.09	1.76	2.48	2.92	1.92
Std. room 1	21.7	10.2	11.8	10.9	12.2	13.2	8.28
Std. room 2	13.2	7.03	8.73	8.63	8.68	10.7	6.57
(C) Transition types	1 fish	2 fish	3 fish	5 fish	7 fish	10 fish	20 fish
Collective	32.9	23.1	16.4	19.5	14.0	22.4	6.9
One-by-one	0.1	2.4	3.7	3.3	3.7	7.8	8.8
U-turns	12.0	12.3	7.0	6.9	5.3	5.4	4.5

TABLEAU 6.2 – Standard deviations of the means of (A) majority events, (B) durations, (C) numbers of transition types with a majority of zebrafish in the three sections of the setup.

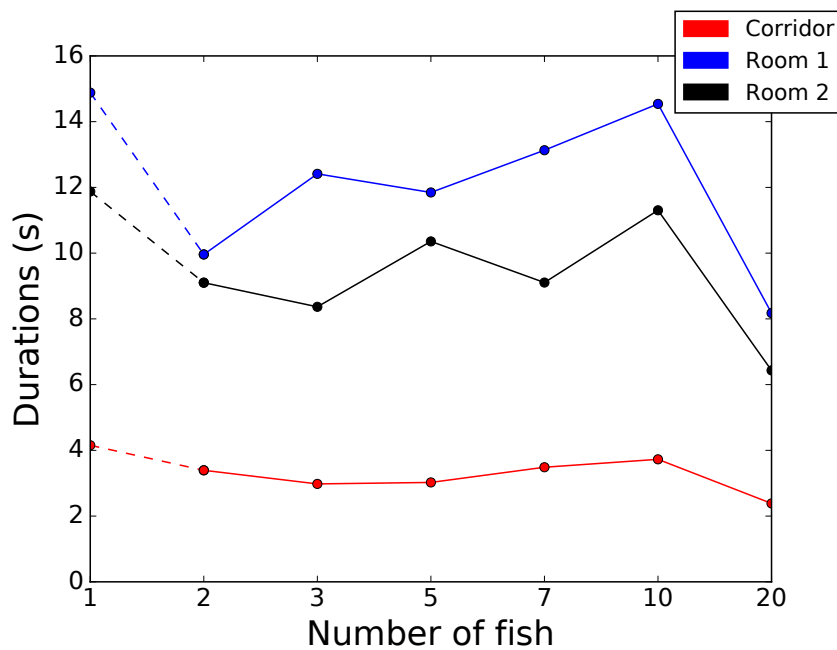


FIGURE 6.18 – Means of the time spent by a majority of fish in each area. The results correspond to 12 replicates of 1 hour. The red line represents durations in the corridor, the blue line the durations in the room 1 and the black line the durations in the room 2. The dashed lines distinguish the experiments with one fish from the experiments with groups of fish. We show that the means of the durations are quite similar in rooms 1 and 2. They are shorter in the corridor than in both rooms. Increasing the size of the groups has no effect on the means of the durations in the corridor when it is generally followed by higher durations in both rooms. Finally, the durations strongly decrease when zebrafish are grouped by 20.

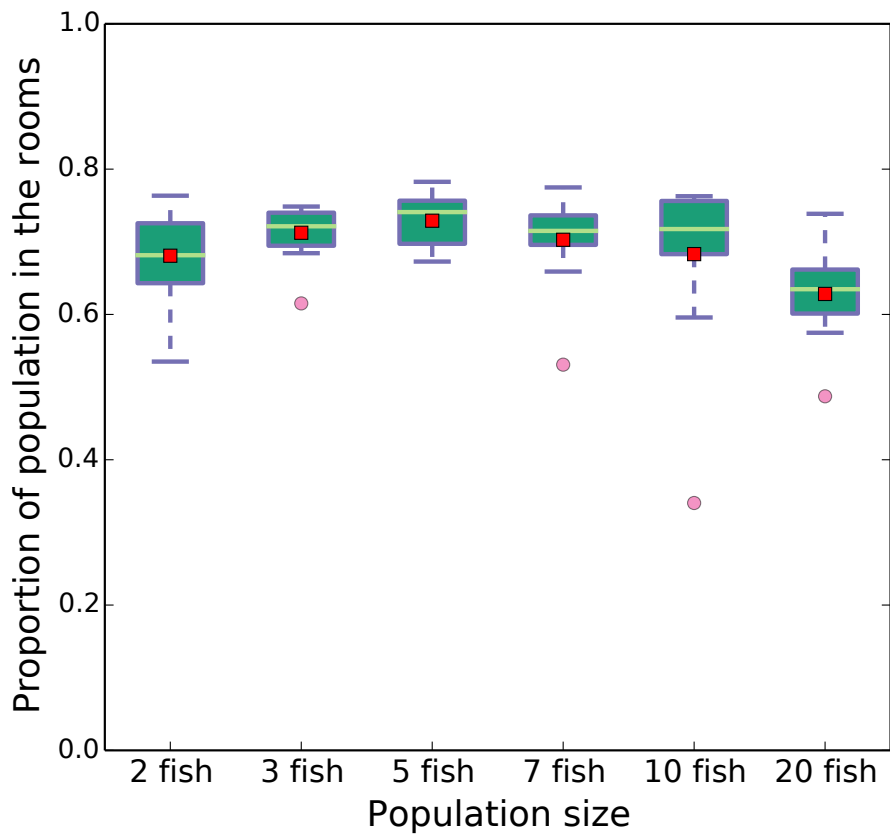


FIGURE 6.19 – **Proportion of fish detected in both rooms.** We show that on average 70% of the fish are detected in the rooms whatever the size of the population. The red square shows the mean and the lighter line the median. We compared the distributions with Kolmogorov-Smirnov tests and found a p -value < 0.001 when comparing the distributions of population sizes of 2 fish versus 20 fish and 3 versus 20. The others comparisons of the distributions were always non significantly different.

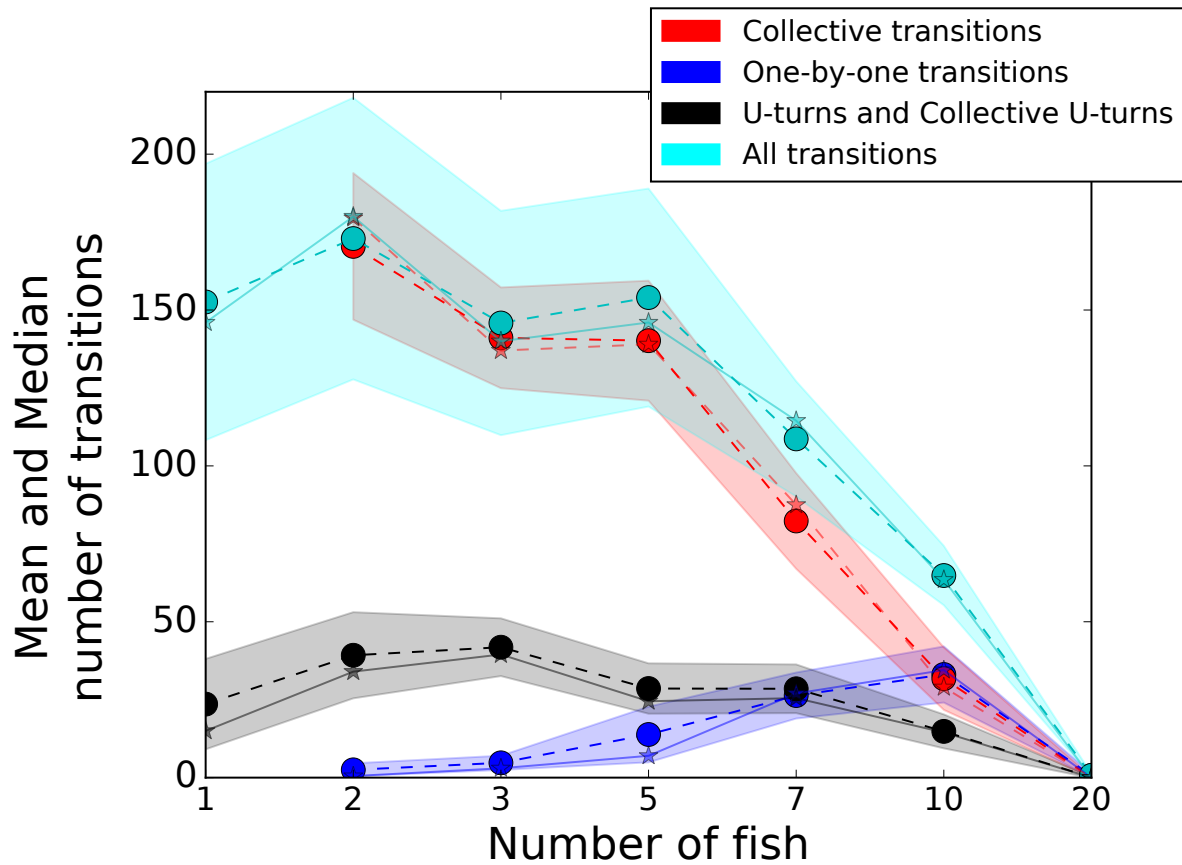


FIGURE 6.20 – **Mean and median number of transitions for different group densities** when all the fish start to move from a room. The red curve shows *Collective transitions*, the blue curve shows *One-by-one transitions*, the black curve represents the *Collective U-turns* and the magenta (*All transitions*) is the sum of *Collective transitions* and *One-by-one transitions*. The dots show the means and the stars the medians. *One-by-one transitions* occur when the fish transit one by one from one room to the other. *Collective transitions* appear when the group transit between both rooms through the corridor. *Collective U-turns* occur when the group go back to the previous room. The dashed lines facilitate the lecture. The figure shows that increasing the group densities makes the number of *Collective U-turns* and *Collective transitions* decrease and the number of *One-by-one transitions* increase. Each point shows the median of 12 values.

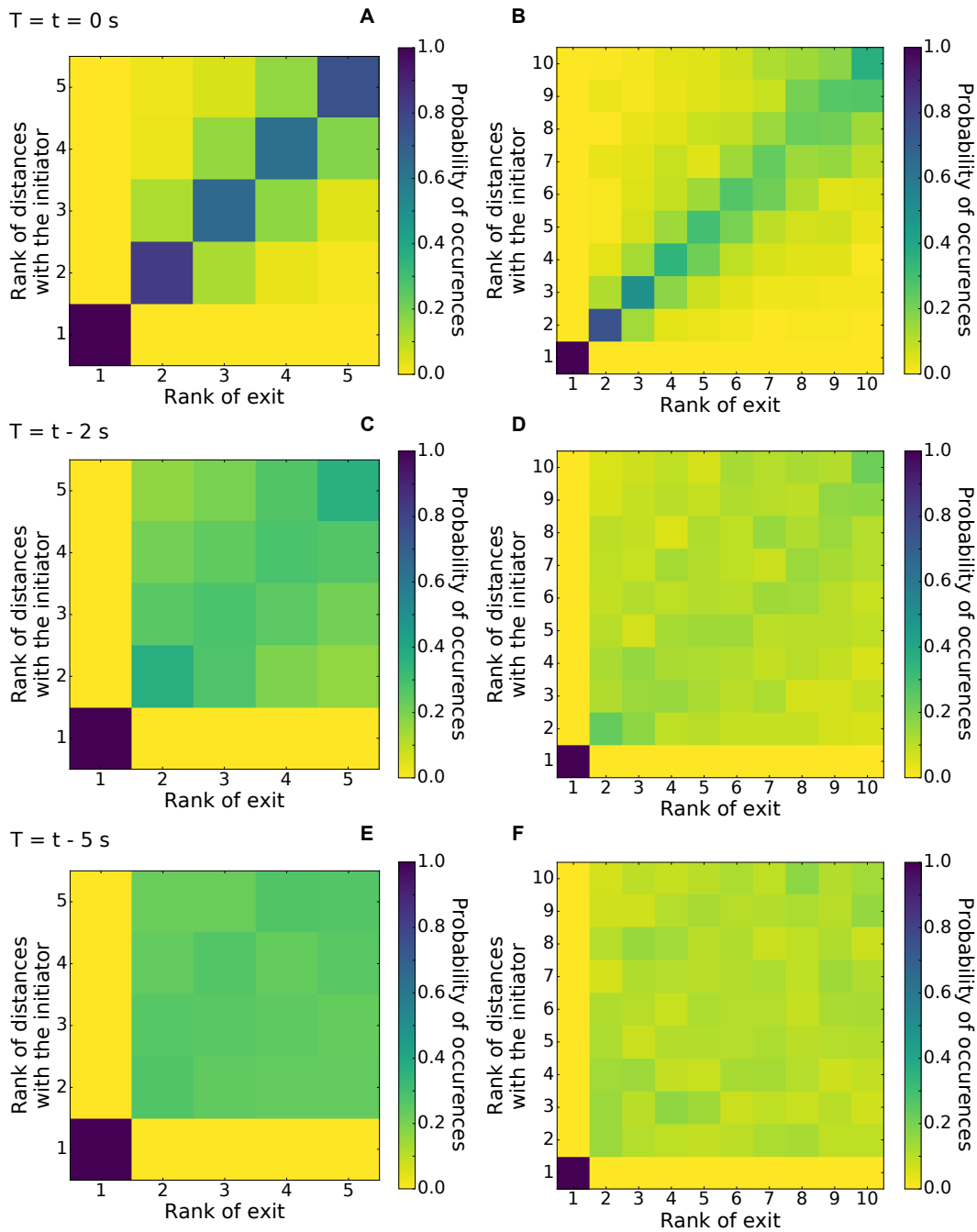


FIGURE 6.21 – **Probability of occurrence of the rank of exit with the rank of distances from the initiator.** The results correspond to groups of 5 zebrafish (left column) and 10 zebrafish (right column). We counted $N = 1456$ exits for 12 replicates with 5 zebrafish and $N = 277$ for 12 replicates with 10 zebrafish. (A) and (B) show the map at the time where the initiator leave the room, (C) and (D) 2 seconds before, (E) and (F) 5 seconds before. As an example, in (A) the probability of occurrence where the second fish leaves the room and has the shortest distance from the initiator is 0.82. As an example, (A) fish with rank of 2 for exit and for distances (closest distance with the initiator) show a probability of 0.82 to be the closest fish to the initiator. This probability decreases to 0.12 for fish with rank of 2 for exit and rank of 3 for distances (the second closest distance with the initiator). Focusing now on (C), 2 seconds before the initiation : the first probability decreases from 0.82 to 0.37 when the second one increases from 0.12 to 0.26. Plots for experiments with 3 and 7 zebrafish are also in the annexe Figure 6.22.

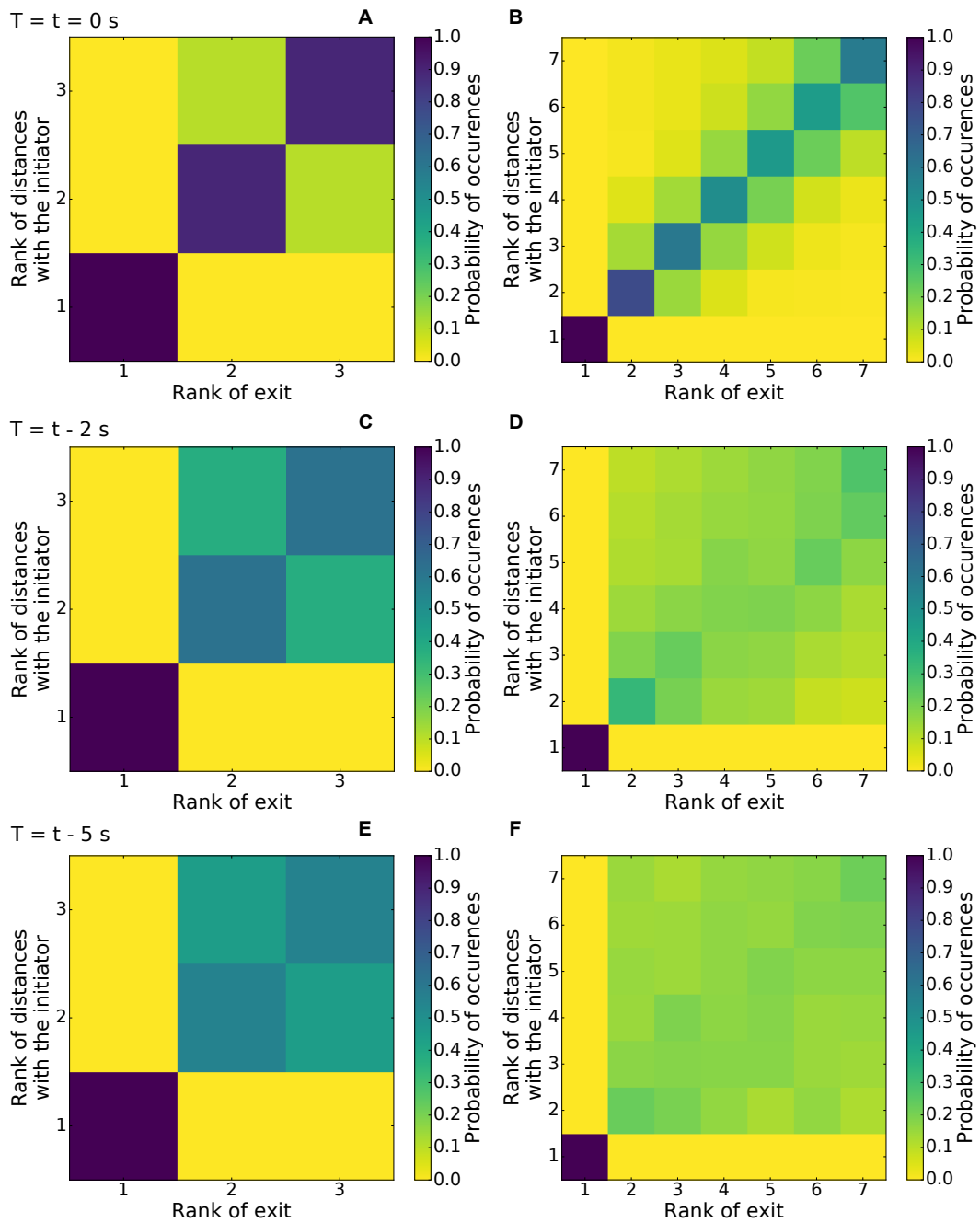


FIGURE 6.22 – **Probability of occurrence of the rank of exit with the rank of distances from the initiator.** The results correspond to groups of 3 zebrafish (left column) and 7 zebrafish (right column). We counted $N = 2195$ exits for 12 replicates with 3 zebrafish and $N = 1020$ for 12 replicates with 7 zebrafish. (A) and (B) show the map at the time where the initiator leave the room, (C) and (D) 2 seconds before, (E) and (F) 5 seconds before.

6.8 Références

- Amé, J.-M., J. Halloy, C. Rivault, C. Detrain et J. L. Deneubourg. 2006, «Collegial decision making based on social amplification leads to optimal group formation», *Proceedings of the National Academy of Sciences*, vol. 103, n° 15, p. 5835–5840. [85](#)
- Arunachalam, M., M. Raja, C. Vijayakumar, P. Malaïammal et R. L. Mayden. 2013, «Natural history of zebrafish (*Danio rerio*) in india», *Zebrafish*, vol. 10, n° 1, p. 1–14. [86](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini et collab.. 2008, «Interaction ruling animal collective behavior depends on topological rather than metric distance : Evidence from a field study», *Proceedings of the national academy of sciences*, vol. 105, n° 4, p. 1232–1237. [100](#)
- Becco, C., N. Vandewalle, J. Delcourt et P. Poncin. 2006, «Experimental evidences of a structural and dynamical transition in fish school», *Physica A : Statistical Mechanics and its Applications*, vol. 367, p. 487–493. [85](#)
- Bourjade, M., B. Thierry, M. Hausberger et O. Petit. 2015, «Is leadership a reliable concept in animals? an empirical study in the horse», *PloS one*, vol. 10, n° 5, p. e0126344. [85](#)
- Bourjade, M., B. Thierry, M. Maumy et O. Petit. 2009, «Decision-making in przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements», *Ethology*, vol. 115, n° 4, p. 321–330. [85](#)
- Branson, K., A. A. Robie, J. Bender, P. Perona et M. H. Dickinson. 2009, «High-throughput ethomics in large groups of drosophila», *Nature methods*, vol. 6, n° 6, p. 451–457. [100](#)
- Briard, L., C. Dorn et O. Petit. 2015, «Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses», *Ethology*, vol. 121, n° 9, p. 888–902. [96](#), [98](#)
- Burd, M. et N. Aranwela. 2003, «Head-on encounter rates and walking speed of foragers in leaf-cutting ant traffic», *Insectes Sociaux*, vol. 50, n° 1, p. 3–8. [95](#)
- Burns, A. L., J. E. Herbert-Read, L. J. Morrell et A. J. Ward. 2012, «Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments», *PLoS One*, vol. 7, n° 5, p. e36567. [96](#)
- Byrne, R., A. Whiten et S. Henzi. 1990, «Social relationships of mountain baboons : Leadership and affiliation in a non-female-bonded monkey», *American Journal of Primatology*, vol. 20, n° 4, p. 313–329. [98](#)
- Chowdhury, D., A. Schadschneider et K. Nishinari. 2005, «Physics of transport and traffic phenomena in biology : from molecular motors and cells to organisms», *Physics of Life reviews*, vol. 2, n° 4, p. 318–352. [95](#)

- Collignon, B., A. Séguret et J. Halloy. 2016, «A stochastic vision-based model inspired by zebrafish collective behaviour in heterogeneous environments», *Royal Society open science*, vol. 3, n° 1, p. 150473. [86](#), [95](#)
- Conradt, L. et T. J. Roper. 2005, «Consensus decision making in animals», *Trends in ecology & evolution*, vol. 20, n° 8, p. 449–456. [85](#)
- Couzin, I. D., J. Krause, N. R. Franks et S. A. Levin. 2005, «Effective leadership and decision-making in animal groups on the move», *Nature*, vol. 433, n° 7025, p. 513–516. [85](#)
- Croft, D., B. Arrowsmith, J. Bielby, K. Skinner, E. White, I. D. Couzin, A. Magurran, I. Ramnarine et J. Krause. 2003, «Mechanisms underlying shoal composition in the trinidadian guppy, *Poecilia reticulata*», *Oikos*, vol. 100, n° 3, p. 429–438. [97](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*Danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [85](#)
- Dankert, H., L. Wang, E. D. Hoopfer, D. J. Anderson et P. Perona. 2009, «Automated monitoring and analysis of social behavior in drosophila», *Nature methods*, vol. 6, n° 4, p. 297–303. [100](#)
- Egan, R. J., C. L. Bergner, P. C. Hart, J. M. Cachat, P. R. Canavello, M. F. Elegante, S. I. Elkhayat, B. K. Bartels, A. K. Tien, D. H. Tien et collab.. 2009, «Understanding behavioral and physiological phenotypes of stress and anxiety in zebrafish», *Behavioural brain research*, vol. 205, n° 1, p. 38–44. [95](#)
- Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan et D. M. Parichy. 2007, «Timing and plasticity of shoaling behaviour in the zebrafish, *Danio rerio*», *Animal behaviour*, vol. 74, n° 5, p. 1269–1275. [84](#), [85](#), [86](#)
- Engeszer, R. E., M. J. Ryan et D. M. Parichy. 2004, «Learned social preference in zebrafish», *Current Biology*, vol. 14, n° 10, p. 881–884. [85](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [85](#)
- Harcourt, J. L., T. Z. Ang, G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Social feedback and the emergence of leaders and followers», *Current Biology*, vol. 19, n° 3, p. 248–252. [85](#)
- Hemelrijk, C. K. et H. Hildenbrandt. 2012, «Schools of fish and flocks of birds : their shape and internal structure by self-organization», *Interface focus*, p. rsfs20120025. [84](#)
- Herbert-Read, J. E., S. Krause, L. Morrell, T. Schaerf, J. Krause et A. Ward. 2013, «The role of individuality in collective group movement», dans *Proc. R. Soc. B*, vol. 280, The Royal Society, p. 20122564. [85](#), [96](#)

- Herbert-Read, J. E., A. Perna, R. P. Mann, T. M. Schaerf, D. J. Sumpter et A. J. Ward. 2011, «Inferring the rules of interaction of shoaling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18 726–18 731. [84](#)
- Hoare, D., I. D. Couzin, J.-G. Godin et J. Krause. 2004, «Context-dependent group size choice in fish», *Animal Behaviour*, vol. 67, n° 1, p. 155–164. [85](#)
- Hoare, D., J. Krause, N. Peuhkuri et J.-G. Godin. 2000, «Body size and shoaling in fish», *Journal of Fish Biology*, vol. 57, n° 6, p. 1351–1366. [97](#)
- Kendall, M. G. 1938, «A new measure of rank correlation», *Biometrika*, vol. 30, n° 1/2, p. 81–93. [101](#)
- King, A. J., C. Sueur, E. Huchard et G. Cowlshaw. 2011, «A rule-of-thumb based on social affiliation explains collective movements in desert baboons», *Animal Behaviour*, vol. 82, n° 6, p. 1337–1345. [96](#)
- King, A. J., L. J. Williams et C. Mettke-Hofmann. 2015, «The effects of social conformity on gouldian finch personality», *Animal Behaviour*, vol. 99, p. 25–31. [96](#)
- Kistler, C., D. Heggin, H. Würbel et B. König. 2011, «Preference for structured environment in zebrafish (*Danio rerio*) and checker barbs (*Puntius oligolepis*)», *Applied Animal Behaviour Science*, vol. 135, n° 4, p. 318–327. [85](#)
- Krause, J. et G. D. Ruxton. 2002, *Living in groups*, Oxford University Press. [97](#)
- Leblond, C. et S. G. Reeb. 2006, «Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [85](#), [98](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [98](#)
- Magnhagen, C. et N. Bunnefeld. 2009, «Express your personality or go along with the group : what determines the behaviour of shoaling perch?», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1671, p. 3369–3375. [96](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danio-nin fishes, including the zebrafish *Danio rerio*», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [86](#)
- Miller, N., S. Garnier, A. T. Hartnett et I. D. Couzin. 2013, «Both information and social cohesion determine collective decisions in animal groups», *Proceedings of the National Academy of Sciences*, vol. 110, n° 13, p. 5263–5268. [85](#)
- Miller, N. et R. Gerlai. 2007, «Quantification of shoaling behaviour in zebrafish (*Danio rerio*)», *Behavioural brain research*, vol. 184, n° 2, p. 157–166. [100](#)

- Miller, N. Y. et R. Gerlai. 2011, «Shoaling in zebrafish : what we don't know», *Reviews in the Neurosciences*, vol. 22, n° 1, p. 17–25. [100](#)
- Nakayama, S., J. L. Harcourt, R. A. Johnstone et A. Manica. 2012a, «Initiative, personality and leadership in pairs of foraging fish», *PLoS One*, vol. 7, n° 5, p. e36606. [85](#)
- Nakayama, S., R. A. Johnstone et A. Manica. 2012b, «Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish», *PLoS One*, vol. 7, n° 8, p. e43747. [96](#)
- Nakayama, S., A. F. Ojanguren et L. A. Fuiman. 2011, «Process-based approach reveals directional effects of environmental factors on movement between habitats», *Journal of Animal Ecology*, vol. 80, n° 6, p. 1299–1304. [85](#)
- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [85](#)
- Oliveira, R. F. 2014, «Mind the fish : zebrafish as a model in cognitive social neuroscience», *Frontiers in neural circuits*. [85](#)
- Parichy, D. M. 2015, «Advancing biology through a deeper understanding of zebrafish ecology and evolution», *ELife*, vol. 4, p. e05635. [86](#)
- Parrish, J. K., S. V. Viscido et D. Grünbaum. 2002, «Self-organized fish schools : an examination of emergent properties», *The biological bulletin*, vol. 202, n° 3, p. 296–305. [84](#)
- Pérez-Escudero, A., J. Vicente-Page, R. C. Hinz, S. Arganda et G. G. de Polavieja. 2014, «idtracker : tracking individuals in a group by automatic identification of unmarked animals», *Nature methods*, vol. 11, n° 7, p. 743–748. [100](#), [101](#), [111](#)
- Petit, O. et R. Bon. 2010, «Decision-making processes : the case of collective movements», *Behavioural Processes*, vol. 84, n° 3, p. 635–647. [84](#)
- Petit, O., J. Gautrais, J.-B. Leca, G. Theraulaz et J.-L. Deneubourg. 2009, «Collective decision-making in white-faced capuchin monkeys», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1672, p. 3495–3503. [98](#)
- Pettersson, L. B. et C. Brönmark. 1993, «Trading off safety against food : state dependent habitat choice and foraging in crucian carp», *Oecologia*, vol. 95, n° 3, p. 353–357. [85](#)
- Pillot, M. H., J. Gautrais, J. Gouello, P. Michelena, R. Bon et collab.. 2010, «Moving together : Incidental leaders and naïve followers», *Behavioural Processes*, vol. 83, n° 3, p. 235–241. [98](#)
- Pritchard, V. L., J. Lawrence, R. K. Butlin et J. Krause. 2001, «Shoal choice in zebrafish, danio rerio : the influence of shoal size and activity», *Animal Behaviour*, vol. 62, n° 6, p. 1085–1088. [85](#), [86](#)
- Radakov, D. V. 1973, «Schooling in the ecology of fish», . [84](#)

- Rieucan, G., J. Morand-Ferron et L.-A. Giraldeau. 2010, «Group size effect in nutmeg mannikin : between-individuals behavioral differences but same plasticity», *Behavioral Ecology*, p. arq039. [85](#)
- Rosenthal, S. B., C. R. Twomey, A. T. Hartnett, H. S. Wu et I. D. Couzin. 2015, «Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion», *Proceedings of the National Academy of Sciences*, vol. 112, n° 15, p. 4690–4695. [85](#), [98](#)
- Séguret, A., B. Collignon et J. Halloy. 2016, «Strain differences in the collective behaviour of zebrafish (*Danio rerio*) in heterogeneous environment», *Royal Society open science*, vol. 3, n° 10, p. 160451. [86](#), [95](#), [96](#)
- Sison, M. et R. Gerlai. 2010, «Associative learning in zebrafish (*Danio rerio*) in the plus maze», *Behavioural brain research*, vol. 207, n° 1, p. 99–104. [85](#)
- Spence, R., M. Fatema, M. Reichard, K. Huq, M. Wahab, Z. Ahmed et C. Smith. 2006, «The distribution and habitat preferences of the zebrafish in bangladesh», *Journal of Fish Biology*, vol. 69, n° 5, p. 1435–1448. [86](#)
- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, *Danio rerio*», *Biological Reviews*, vol. 83, n° 1, p. 13–34. [86](#)
- Strandburg-Peshkin, A., C. R. Twomey, N. W. Bode, A. B. Kao, Y. Katz, C. C. Ioannou, S. B. Rosenthal, C. J. Torney, H. S. Wu, S. A. Levin et collab.. 2013, «Visual sensory networks and effective information transfer in animal groups», *Current Biology*, vol. 23, n° 17, p. R709–R711. [100](#)
- Sueur, C., J.-L. Deneubourg et O. Petit. 2011a, «From the first intention movement to the last joiner : macaques combine mimetic rules to optimize their collective decisions», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 278, n° 1712, p. 1697–1704. [84](#)
- Sueur, C., A. J. King, L. Conradt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C. M. Schaffner, L. Williams, D. Zinner et F. Aureli. 2011b, «Collective decision-making and fission–fusion dynamics : a conceptual framework», *Oikos*, vol. 120, n° 11, p. 1608–1617. [84](#), [97](#)
- Sueur, C. et O. Petit. 2008, «Organization of group members at departure is driven by social structure in macaca», *International Journal of Primatology*, vol. 29, n° 4, p. 1085–1098. [96](#)
- Sueur, C., O. Petit et J.-L. Deneubourg. 2009, «Selective mimetism at departure in collective movements of macaca tonkeana : an experimental and theoretical approach», *Animal Behaviour*, vol. 78, n° 5, p. 1087–1095. [96](#)
- Suriyampola, P. S., D. S. Shelton, R. Shukla, T. Roy, A. Bhat et E. P. Martins. 2016, «Zebrafish social behavior in the wild», *Zebrafish*, vol. 13, n° 1, p. 1–8. [86](#)

- Tunstrøm, K., Y. Katz, C. C. Ioannou, C. Huepe, M. J. Lutz et I. D. Couzin. 2013, «Collective states, multistability and transitional behavior in schooling fish», *PLoS Comput Biol*, vol. 9, n° 2, p. e1002915. [85](#)
- Ward, A. J., J. E. Herbert-Read, L. A. Jordan, R. James, J. Krause, Q. Ma, D. I. Rubenstein, D. J. Sumpter et L. J. Morrell. 2013, «Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish», *The American Naturalist*, vol. 181, n° 6, p. 748–760. [85](#), [97](#)
- Ward, A. J., J. E. Herbert-Read, D. J. Sumpter et J. Krause. 2011, «Fast and accurate decisions through collective vigilance in fish shoals», *Proceedings of the National Academy of Sciences*, vol. 108, n° 6, p. 2312–2315. [85](#)
- Wiens, J. A. 1976, «Population responses to patchy environments», *Annual review of ecology and systematics*, p. 81–120. [86](#)

Chapitre 7

Collective departures in zebrafish : profiling the initiators

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In review

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7.1 Résumé

Chez les animaux sociaux, une des questions fondamentales porte sur la compréhension des mécanismes décisionnels qui dirigent le groupe lors de ses déplacements tout en préservant sa cohésion. Ici, nous analysons les initiations de départs collectifs du zebrafish, *Danio rerio*. Nous observons des populations de 2, 3, 5, 7 et 10 individus nageant dans une arène constituée de deux salles connectées par un couloir et quantifions les initiations des départs collectifs. Alors que tous les poissons initient au moins une fois un départ collectif, il ressort que certains individus en initient plus souvent que d'autres. Nous montrons que le nombre d'initiations effectives est proportionnel au nombre de tentatives d'initiations et que tous les poissons présentent le même taux de succès d'initiation après une tentative. De plus, nous notons une corrélation positive entre le classement des poissons pour les initiations effectuées et le classement des poissons pour leur vitesse moyenne de nage. Tous ces résultats nous suggèrent que l'initiation des départs collectifs chez les zebrafish est un processus hétérogène quand bien même tous les individus ont la même chance de réussir une initiation après une tentative d'initiation.

7.2 Abstract

For animals living in groups, one of the important questions is to understand what are the decision-making mechanisms that lead to choosing a motion direction or leaving an area while preserving group cohesion. Here, we analyse the initiation of collective departures in zebrafish *Danio rerio*. In particular, we observed groups of 2, 3, 5, 7 and 10 zebrafish swimming in a two resting sites arena and quantify the number of collective departure initiated by each fish. While all fish initiated at least one departure, the probability to be the first one to exit a resting site is not homogeneously distributed with some individuals leading more departures than others. We show that the number of initiation is linearly proportional to the number of attempts performed and that all fish have the same success rate to lead the group out of a resting sites after an attempt. In addition, by measuring the average swimming speed of all fish, we highlight that the intra-group ranking of a fish for its proportion of initiation is correlated to its intra-group ranking in average speed. These results highlight that the initiation of collective departure in zebrafish is a heterogeneously distributed process, even if all individuals have the same success rate after attempting a departure.

7.3 Introduction

Collective departure is a decision-making faced by all social species that travel in groups. In this process, an individual generally initiates the movement of the group out of a residence site or towards a new direction. The identity and motivation of this initiator can widely vary according to the social organisation of the considered species [Ward et collab. \[2013\]](#). On the one hand, the leadership is often assumed by a unique or a subset of individuals that monopolise the decisions in hierarchical societies. These individuals can be older [Sueur et Petit \[2008\]](#), dominant [Peterson et collab. \[2002\]](#); [Sueur et Petit \[2008\]](#) or of a specific sex [Anne et Rasa \[1983\]](#). These characteristics are generally long-lasting and result in a consistent leadership over time, generally observed in stable and closed groups. On the other hand, the initiators can also be temporarily more motivated due to their physiological state [Fischhoff et collab. \[2007\]](#); [Sueur et collab. \[2010\]](#), level of information [Collignon et Detrain \[2010\]](#); [Couzin et collab. \[2011, 2005\]](#); [Pillot et collab. \[2010\]](#) or position in the group [Bumann et Krause \[1993\]](#); [Leca et collab. \[2003\]](#). In these cases, the initiation can be done by any individual of the group without consistency over time. This mechanism is often present in social species that live in open groups with no consistent membership like bird flocks or fish schools.

Although each individual can initiate collective movement in these more egalitarian societies, some characteristics may enhance the probability of some members to take the leadership. For example, bold individuals that have a higher tendency to explore new areas will more often lead departures [Leblond et Reeb \[2006\]](#). Similarly, group members with higher nutritional needs will be more motivated to initiate movements towards foraging spots [Rands et collab. \[2003\]](#). Therefore, even in non-hierarchical species, leadership can be heterogeneously distributed among the group members. In this context, we studied the distribution of the leadership in the zebrafish *Danio rerio*. In its natural habits, *Danio rerio* is a gregarious species that live in small groups (a few to a dozen individuals) in shallow freshwaters [Engeszer et collab. \[2007b\]](#); [McClure et collab. \[2006\]](#); [Parichy \[2015\]](#); [Spence et collab. \[2008\]](#). It is a well known model animal in genetics and neuroscience [Norton et Bally-Cuif \[2010\]](#) but also in ethology.

Indeed, zebrafish has become a common organism for research on individual and collective behaviours. Studies have shown that a continuum from shy (less risk-prone) to bold (risk takers) individuals can be observed in zebrafish shoals [Dahlbom et collab. \[2011\]](#). This inter-individual variability is correlated with the social status of the fish, bold individuals being more often dominant [Dahlbom et collab. \[2011\]](#), aggressive and having potentially a higher reproductive success [Ariyomo et Watt \[2012\]](#). At the collective level, the shoaling behaviour of zebrafish is already observed in larvae and shoaling preferences appear at the juvenile stage [Engeszer et collab. \[2007a\]](#). In adults, zebrafish periodically

oscillate from loosely connected groups to dense aggregates [Miller et Gerlai \[2008\]](#) and regularly transit from unstructured shoals to polarised schools (and inversely). During the school phases, the zebrafish show a larger inter-individual distances and swim at a higher speed [Miller et Gerlai \[2012\]](#). Thus, groups of zebrafish show a succession of mobile and static phases.

Here, our goal is to study the initiation of such repeated short-term collective movements and the presence of leaders during successive collective departures. To do so, we observe groups of 2, 3, 5, 7 and 10 zebrafish swimming in an experimental arena consisting of two rooms connected by a corridor. We expect the zebrafish to collectively rest in one of the two rooms and regularly transit towards the other one. Our aim is to measure the number of collective departure initiated by each fish and to put in relation their propensity to lead departures with the number of attempts that they made as well as their swimming speed.

7.4 Methods

7.4.1 Ethic statement

Fish experiments were performed in accordance with the recommendations and guidelines of the Buffon Ethical Committee (registered to the French National Ethical Committee for Animal Experiments #40) after submission to the state ethical board for animal experiments.

7.4.2 Animals and housing

The fish were reared in housing facilities ZebTEC and fed two times a day (Special Diets Services SDS-400 Scientific Fish Food). We kept fish under laboratory conditions, 27°C, 500µS salinity with a 10 :14 day :night light cycle. Water pH was maintained at 7 and Nitrites (NO²⁻) are below 0.3 mg/l. All zebrafish observed in this study were 6-12 months old at the time of the experiments.

7.4.3 Experimental setup

We observed groups of zebrafish swimming in an arena consisting of two square rooms connected by a corridor starting at one corners of each room placed in a 100 cm x 100 cm x 30 cm experimental tank (Fig. 8.1). The walls of the arena were made of white opaque PMMA. The water depth was kept at 6 cm during the experiments in order to keep the fish in nearly 2D to facilitate their tracking. One lamp (400W) was placed on the floor at each edge of the tank which is 60 cm above the floor to provide indirect lightning. The whole

setup was confined behind white sheets to isolate experiments and homogenise luminosity. A high resolution camera was mounted 1.60m above the water surface to record the experiment at a resolution of 2048 pixels x 2048 pixels and at 15 frames per second.

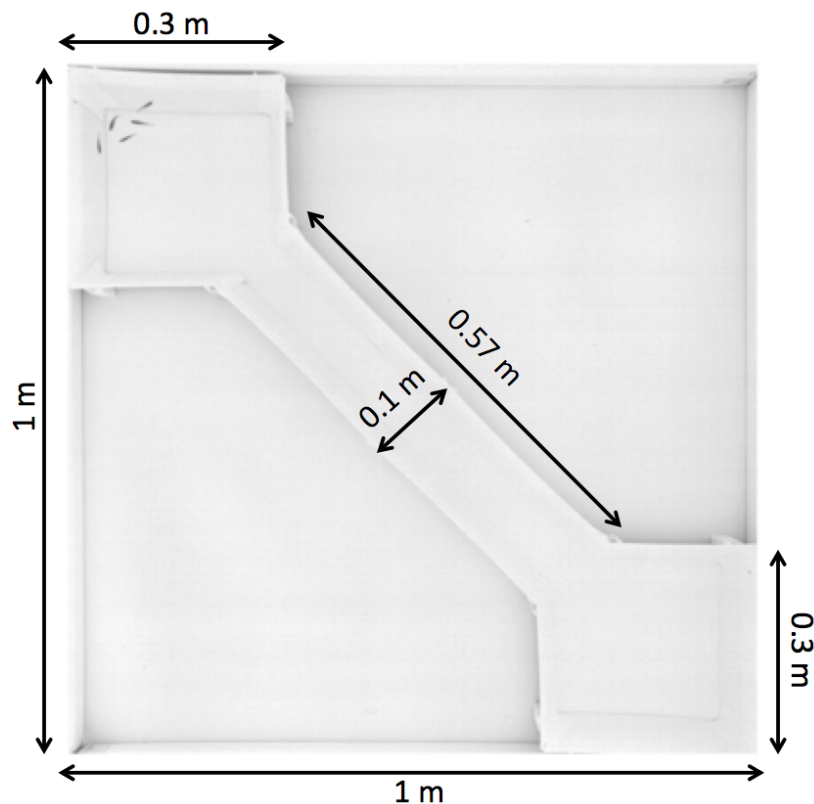


FIGURE 7.1 – Experimental arena composed by two square rooms (30 cm x 30 cm) connected by a corridor (57 cm x 10 cm). The zebrafish were observed swimming during trials of 1 hour to study the collective departures of the fish from one room to the other.

7.4.4 Experimental procedure

We observed 12 groups of two, three, five, seven and ten adult laboratory wild-type zebrafish (*Danio rerio*) AB strain during one hour for a total of 60 experiments. Before the trials, the fish were placed with a hand net in a cylindrical arena (20 cm diameter) in one of the two rooms. Following a 5 minutes acclimatisation period, the camera started recording and the fish were released and able to swim in the experimental arena. After one hour, the fish were caught by a hand net and replaced in the rearing facilities.

7.4.5 Data analysis

The videos were analysed off-line by the idTracker software [Pérez-Escudero et collab. \[2014\]](#). This multi-tracking software extracts specific characteristics of each individual and uses them to identify each fish without tagging throughout the video. This method

avoids error propagation and is able to successfully solve crossing, superposition and occlusion problems. However, the tracking system failed to correctly track one experiment with two fish, one experiment with five fish and two experiments with ten fish. Therefore, these four experiments were excluded from our analysis. For all other experiments, we obtained the coordinates $P(x, y, t)$ of all fish at each time step $\Delta t = 1/15s$. With these coordinates, we built the trajectories of each fish and computed their position in the arena and their instantaneous speed v_t calculated on three positions and computed as the distance between $P(x, y, t - 1)$ and $P(x, y, t + 1)$ divided by two time steps.

7.5 Results

First, we quantified for all the replicates the total number of collective residence events (CRE) defined as the whole group resting in one of the two rooms. The number of CRE decreases when the size of the groups increases with a median number of 233 CRE for 2 fish to 131 CRE for groups of 10 fish (Fig. 7.2A). Then, we counted the total number of collective departures events (CDE) defined as the whole group leaving one of the resting sites for the corridor towards the other one. The number of CDE also decreases but with a stronger difference between the groups from a median number of 212 for two zebrafish to 16 CDE for 10 zebrafish (Fig. 7.2B). Therefore, 90% of the CRE were followed by a collective departure in groups of 2 fish while only 12% were in groups 10 fish (Fig. 7.2C). Thus, larger groups were more likely to split into subgroups during departures while small groups of fish swam together most of the time.

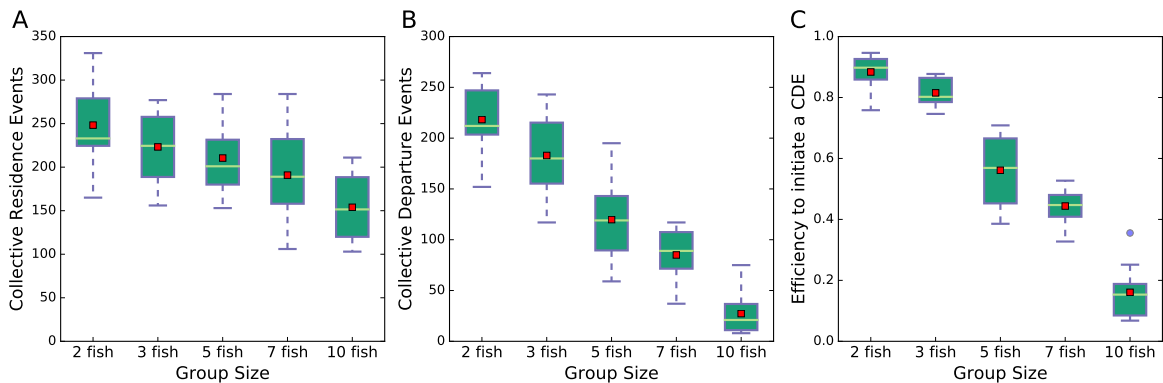


FIGURE 7.2 – (A) Number of collective residence events (CRE) and (B) collective departure events (CDE) for the 11 groups of two, 12 groups of three, 11 groups of five, 12 groups of seven and 10 groups of 10 zebrafish observed during one hour. Collective residence events are defined as the whole group resting in one of the two rooms and collective departures events are defined as the whole group leaving one of the resting sites. (C) Efficiency of the first leaver to trigger a collective departure of all fish computed as the proportion of CRE that were followed by a CDE.

Thanks to the individual tracking of the fish, we were able to determine the identity

of the first fish that left a room for all collective departures. Thus, for all groups, we computed the proportion of collective departure initiated by each fish and ranked the group members according to the proportion of departure that they led. To characterise the distribution of the leadership among the group members, we compared these experimental distributions with two theoretical ones. On the one hand, we simulated a situation where all fish have the same probability ($1/n_{fish}$) to initiate a departure. On the other hand, we simulated a despotic configuration with a fish that has a 0.9 probability to initiate a collective movement while the others have only a $0.1/(n_{fish} - 1)$ chance to start a departure. The experimental data lay between these two extreme scenarios (Fig. 7.3 for groups of 5 fish). In groups of five fish, the 1st ranked fish initiated 45% of the collective departures on average. This value is largely below the 90% observed in the despotic simulation but also higher than the 25% of the uniform repartition. We observed similar results for groups of 2, 3, 7 and 10 fish (see supplementary figures) and compared the distributions of the initiation in each group with a homogeneous distribution by a χ^2 test of goodness of fit. Among the 56 groups, only four groups of 2 fish, one group of 3 fish and 4 groups of 10 fish did not significantly differ from the equal repartition of the leadership (see supplementary table 1 for details). Thus, these results highlight a heterogeneous distribution of leadership among group members (although not despotic) in the large majority of the groups with some fish having a higher tendency to start departure than others.

To determine whether this distributed leadership was related to a different success rate or to a different number of initiation attempts, we measured the number of time that each fish was the first to exit a resting site independently of its success to be followed by the other group members (defined as an *attempt*). For each group, we compared the distribution of the total number of attempts made by each fish with a theoretical homogeneous distribution. For two fish, 4 dyads out of 11 did not significantly differ from the homogeneous distribution (χ^2 test of goodness of fit with a homogeneous distribution, see supplementary table 2 for details). In groups of three fish, the hypothesis of homogeneous distribution was not rejected in only one trio. Finally, all groups of 5, 7 and 10 fish significantly differ from the equal distribution of the number of attempts. In addition, we computed the proportion of attempts made by each fish and ranked them according to their score. We also ranked each group according to the level of deviation from the homogeneous distribution (measured by the p -value of the χ^2 test). These rankings show the presence of a continuum from an more egalitarian to a more despotic distribution for all group sizes (Fig. 7.4). Thus, like the distribution of initiations, the attempts are generally heterogeneously distributed among the fish of a group.

Therefore, we analysed the potential correlation between the number of initiations and the number of attempts made by each fish. A linear regression shows that the number of initiation is linearly correlated to the number of attempts perform by the fish and

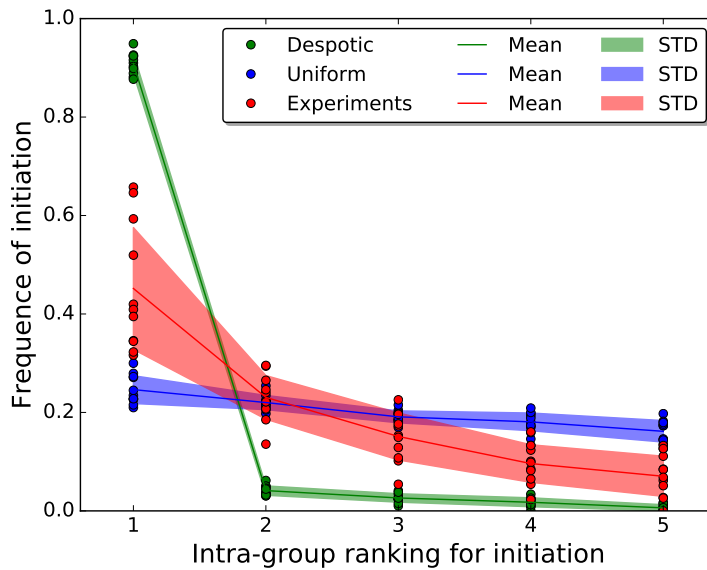


FIGURE 7.3 – Frequency of initiation according to the intra-group ranking of the fish in groups of 5 individuals. For each group, we calculated the proportion of departure initiated by each fish and ranked them according to this frequency. The experimental results (in red) are compared with a simulated distributions (uniform in blue and despotic in green). The uniform distribution assumed that the fish have the same probability $p = 0.2$ to initiate a collective departure while the despotic distribution assumed that one fish has a probability $p = 0.9$ and the other a probability $p = 0.025$ to initiate a departure.

that the coefficient of this correlation depends on the group size (Fig. 7.5A). For groups of two fish, 92% of the attempts made by an individual resulted in a collective departure of the dyad. For larger group sizes, the success rate for each attempt decreases when the population increases : 90% for 3 fish, 64% for 5 fish, 53% for 7 fish and 26% for 10 fish. While the probability of group splitting increases with the group size, the linear relation between the numbers of attempts and initiations highlights that this success rate to initiate a collective departure is the same for all fish. This conclusion is confirmed by the intra-group proportion of initiation led that is equal to the proportion of attempts performed by each fish (Fig. 7.5B). Thus, the higher status of initiator of some fish is not related to a higher influence on other group members or a better success rate but on a higher tendency to exit the resting sites.

Next, we studied the temporal distribution of the leading events to highlight a potential succession of temporary leaders over successive departures. To do so, we computed the probability of a fish to perform two successive initiations and compared this probability to the proportion of CDE that the fish has led. A temporal segregation of the initiators would result in a high probability of successive initiations compared to the proportion of led CDE while homogeneously distributed initiations would give similar probabilities

of successive initiations and led CDE. For all group sizes, we observed a linear correlation between the two proportions (Fig. 7.6). Thus, the probability of a fish to initiate a CDE was not dependent on its status of initiator or follower during the previous CDE.

Finally, we looked at a potential link between the motion characteristics of the individual and the number of attempts that they have made. In particular, we measured the average linear speed of all individuals as an indicator of their motility. There is a positive correlation between the average speed of the fish and the number of attempts that they performed. However, this correlation is only significant for groups of 5, 7 and 10 fish (Fig. 7.7A-E, Spearman's correlation). As the number of attempts made by a fish depends on the motivation of its groupmates (a potential *good* initiator could be hidden by a *super* initiator), we also compared the intra-group ranking of the fish for the number of initiation with their intra-group ranking for the linear speed. We used the Kendall's τ coefficient to measure the association between the two rankings. The intra-group ranking for the initiation is positively correlated to the intra-group ranking for the linear speed (Fig. 7.7F-J) for groups of 3, 5, 7 and 10 fish. Thus, except for dyads, the fish with the highest average speed of its group is more likely to also be the fish that has started the largest number of departures. These results show that the initiation of collective movements is related to the motility of the fish.

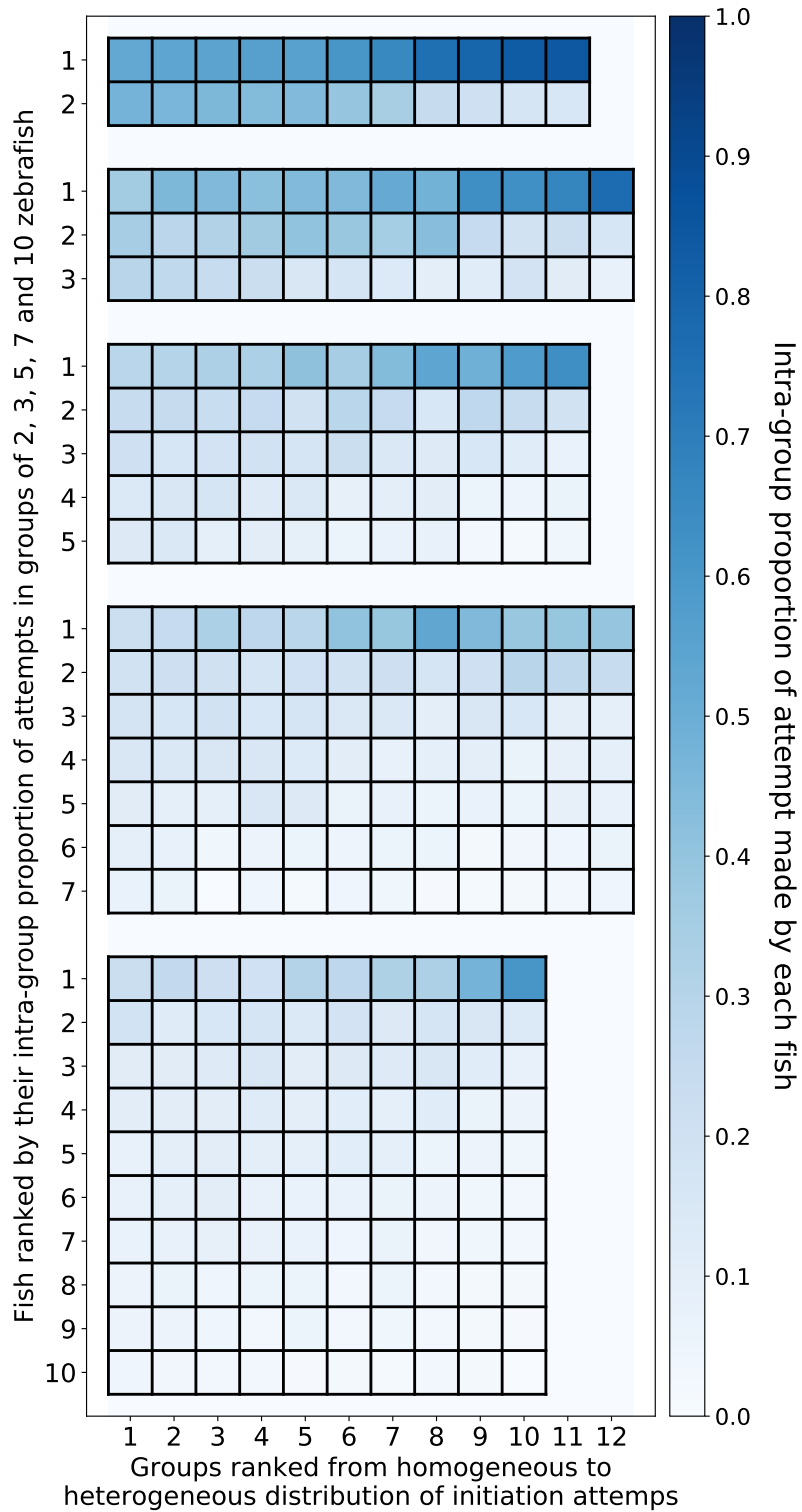


FIGURE 7.4 – Proportion of initiation attempts made by each fish for group of 2, 3, 5, 7 and 10 fish. For each population size, the groups are ranked from the most homogeneous distribution of attempts (left) to the most heterogeneous distribution (right). In each group, the fish are ranked from the highest proportion of attempt (top) to the lowest proportion of attempt (down).

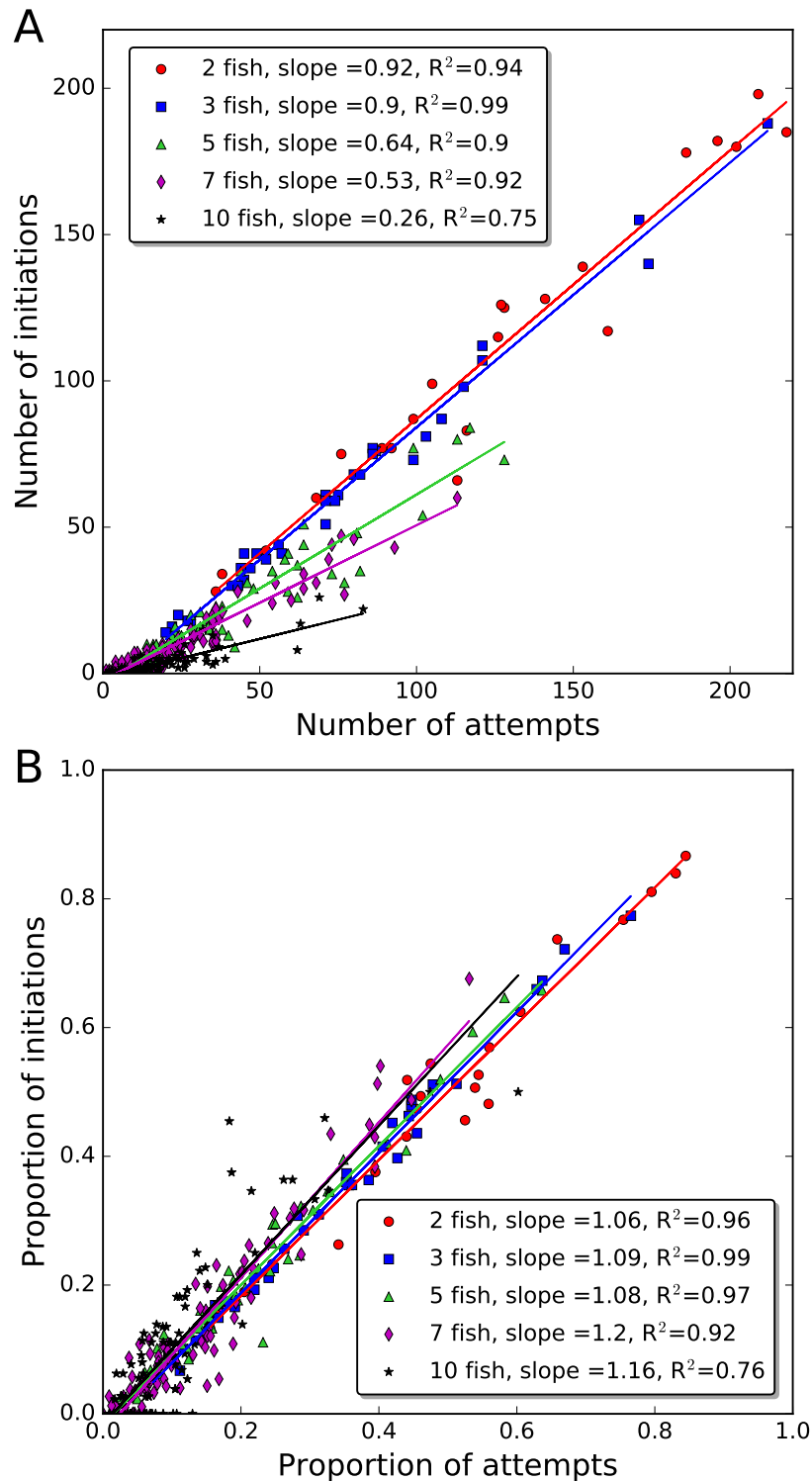


FIGURE 7.5 – (A) The total number of collective departure initiated in relation to the total number of attempts made by fish. The data shows that the number of initiations is directly proportional to the number of attempts. Thus, while the fish widely differ in the total number of attempts/initiations, each fish has the same probability of success to initiate a collective departure when attempting. (B) The proportion of attempts made by the fish in relation to the proportion of departures initiated. The data shows that the proportion of attempts and initiations are similar for all fish.

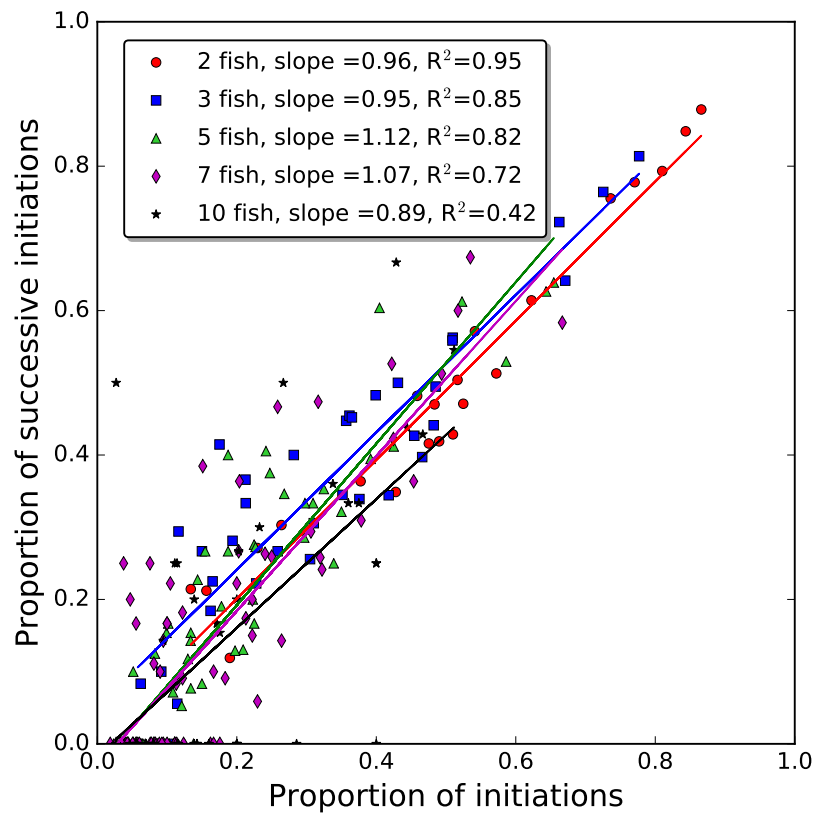


FIGURE 7.6 – Proportion of successive initiations as a function of the proportion of initiated collective departures for 2, 3, 5, 7 and 10 fish. The linear relationship highlight that the leadership events of each fish were homogeneously distributed along the experiment without temporal segregations of the initiators.

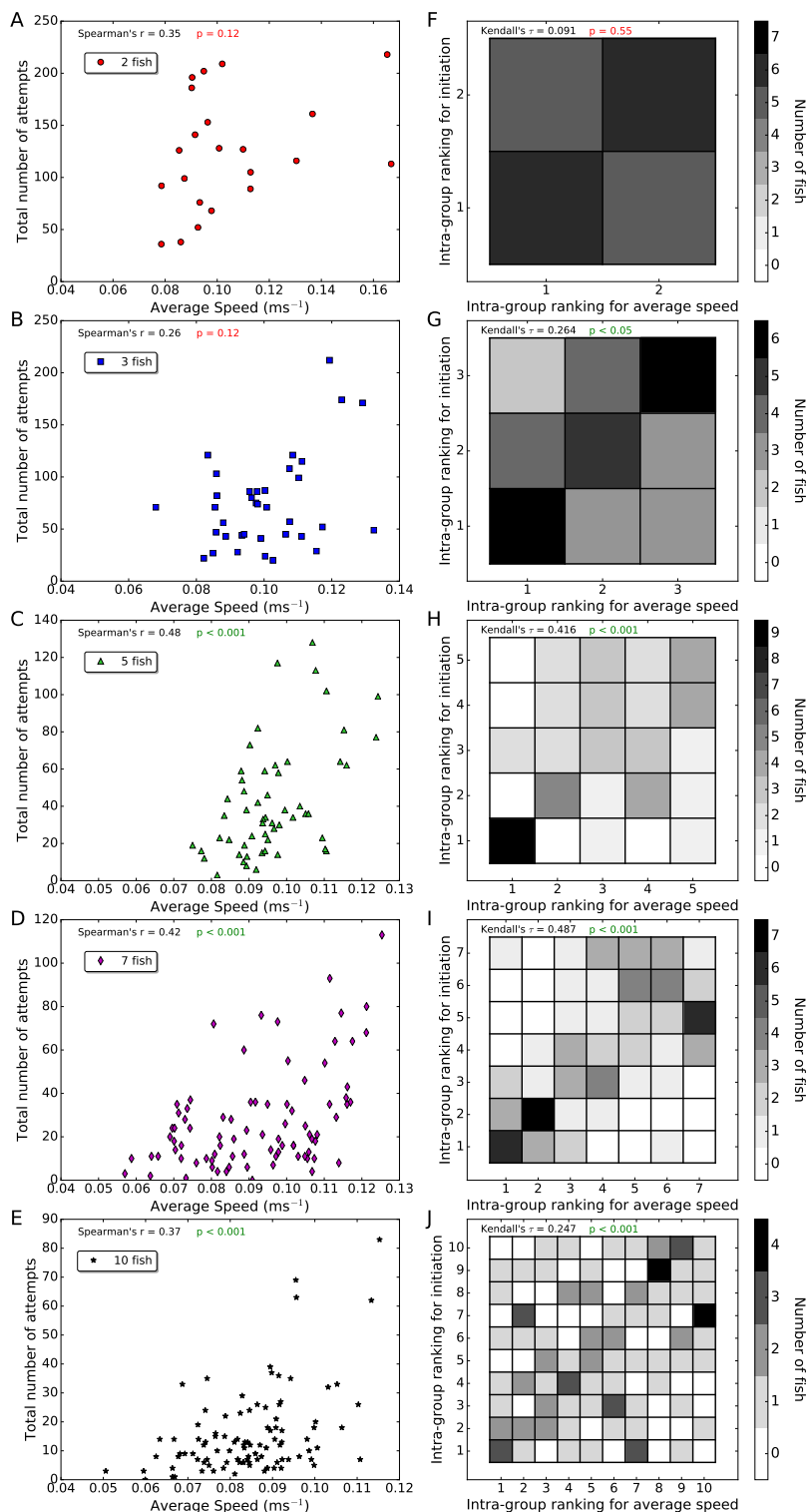


FIGURE 7.7 – (A-E) Proportion of collective departures initiated by each fish according to its average speed. The results show that for small group sizes (2 or 3 fish), the mean linear speed is not a predictor of the proportion of initiation performed by a fish (Sperman's correlation). For larger group size (5, 7 and 10 fish), the linear speed of a fish is positively correlated with the number of attempts that it made. (F-J) Distribution of the fish according to their intra-group ranking of the proportion of collective departure initiated and their intra-group ranking for the average speed.

7.6 Discussion

The initiation of collective movement in fish is often reported as a distributed process in which each fish can potentially lead a departure. This distribution of the leadership is particularly suited for large schools of hundreds or thousands of fish that have to detect and avoid attacks from predators coming potentially from any direction [Krause et collab. \[2000\]](#). Thus, the first fish to spot a predator can start an escaping manoeuvre that will be propagated from neighbour to neighbour in the whole school. Here, we studied the initiation of collective movement in smaller groups of zebrafish *Danio rerio* swimming in an environment composed by two spots in a non-stress situation. In this context, we showed that the initiation of collective departure is a distributed process among the group members. However, the role of initiator is not homogeneously distributed, with some individuals leading more departures than others. By measuring the number of attempt made by each fish, we highlighted that this heterogeneous distribution was not the result of a higher success rate of some individuals that could have a higher tendency to be followed. On the contrary, the success of the fish to trigger a collective departure was linearly correlated to their number of attempt. This result was also observed in other fish species like Damsel fish in which collective departures from one spot to another was mainly led by fish that performed a higher number of attempts [Ward et collab. \[2013\]](#). In addition, we showed that the initiation process was not temporarily organised with a fish leading the group during a particular time period before being relayed by another fish, but was distributed during the whole experimental time between the group members.

Our results also highlighted that the motility of the fish is a predictor of the tendency of the fish to initiate collective departure. Indeed, except for duos, the intra-group ranking of a fish for average speed was correlated to its intra-group ranking for departure's attempts. Therefore, the leaders of collective movements in zebrafish do not seem to occupy a particular hierarchical status in the group but are generally the more mobile individuals. A similar result was predicted by a theoretical analysis on the emergence of leadership in simulated zebrafish [Zienkiewicz et collab. \[2015\]](#). This study showed that an informed individual moving in a specific direction is more likely to be followed by a group of naive individuals when it moves just faster than the naïve group. In Damsel fish, the initiator of a collective movement also displays a higher level of activity than their group member before the departure [Ward et collab. \[2013\]](#). A favored direction, a higher level of activity or a higher average speed can lead a fish to occupy the front position of the shoal more often than its group members. As the direction of the group is mainly decided by the front individuals [Bumann et Krause \[1993\]](#), these inter-individual behavioural differences lead to heterogeneously distributed leadership in the shoal.

Finally, our results also show that the sharing of leadership across the different groups

is a continuum from homogeneously distributed leadership to strongly asymmetrical distributions. In our experiments, dyads showed the most egalitarian situations but also the strongest monopolization of leadership with one fish performing up to 85% of the initiations of its group. A similar result was observed in trios with some groups sharing equally the leadership between all group members and others groups with a disproportionate number of initiation led by the same fish (up to 75% for one group). As the group size increases, almost all groups showed a heterogeneous distribution of the leadership between the fish even if we did not observe a clear monopolization of the initiation of collective departure in these shoals. A similar effect of group size on leader-followers interaction was evidenced in minnows [Partridge \[1980\]](#). In this study, 6 out of 9 dyads displayed a clear leader-follower relation, 2 showed an equally shared leadership and 1 was formed by fish that did not interact with each other. The author thus concluded that one fish leads the other in groups of two fish but that this behaviour is not observed for larger groups.

Thus, stronger asymmetries are more likely to be observed in smaller group sizes but an unbalanced distribution is almost always present in large groups. Such outcome can be the results of sampling of a continuous distribution for an individual characteristic that influences the probability to lead the group. Indeed, as we add more individuals, there is a higher probability that at least two of them significantly differ from each other, leading to a unshared decision-making process but by the same time, the average difference between individuals tend to stabilize to a limit value. On the contrary, as only two fish are forming a dyad, there is a probability that these fish are either almost identical, resulting in a homogeneous leadership, or on the contrary strongly different, leading to a heterogeneous leadership, with a continuum of possibilities between these extrema.

In animal species in which the initiation of specific behaviours is related to individual characteristics rather than to a particular hierarchical position, stronger asymmetries can potentially appear in smaller groups. Thus, while a non-despotic situation prevails in zebrafish, species that form only small groups are more likely to display a whole range of social structure from despotic to egalitarian shoals while larger group will tend to show the same configuration, without any behavioural changes but only due to sampling effects.

7.7 Références

- Anne, O. et E. Rasa. 1983, «Dwarf mongoose and hornbill mutualism in the taru desert, kenya», *Behavioral Ecology and Sociobiology*, vol. 12, n° 3, p. 181–190. [127](#)
- Ariyomo, T. O. et P. J. Watt. 2012, «The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish», *Animal Behaviour*, vol. 83, n° 1, p. 41–46. [127](#)

- Bumann, D. et J. Krause. 1993, «Front individuals lead in shoals of three-spined sticklebacks (*gasterosteus aculeatus*) and juvenile roach (*rutilus rutilus*)», *Behaviour*, vol. 125, n° 3, p. 189–198. [127](#), [138](#)
- Collignon, B. et C. Detrain. 2010, «Distributed leadership and adaptive decision-making in the ant *tetramorium caespitum*», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 277, n° 1685, p. 1267–1273. [127](#)
- Couzin, I. D., C. C. Ioannou, G. Demirel, T. Gross, C. J. Torney, A. Hartnett, L. Conradt, S. A. Levin et N. E. Leonard. 2011, «Uninformed individuals promote democratic consensus in animal groups», *science*, vol. 334, n° 6062, p. 1578–1580. [127](#)
- Couzin, I. D., J. Krause, N. R. Franks et S. A. Levin. 2005, «Effective leadership and decision-making in animal groups on the move», *Nature*, vol. 433, n° 7025, p. 513–516. [127](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [127](#)
- Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan et D. M. Parichy. 2007a, «Timing and plasticity of shoaling behaviour in the zebrafish, *danio rerio*», *Animal behaviour*, vol. 74, n° 5, p. 1269–1275. [127](#)
- Engeszer, R. E., L. B. Patterson, A. A. Rao et D. M. Parichy. 2007b, «Zebrafish in the wild : a review of natural history and new notes from the field», *Zebrafish*, vol. 4, n° 1, p. 21–40. [127](#)
- Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, H. M. Larkin, M.-J. Sellier et D. I. Rubenstein. 2007, «Social relationships and reproductive state influence leadership roles in movements of plains zebra, *equus burchellii*», *Animal Behaviour*, vol. 73, n° 5, p. 825–831. [127](#)
- Krause, J., D. Hoare, S. Krause, C. Hemelrijk et D. Rubenstein. 2000, «Leadership in fish shoals», *Fish and Fisheries*, vol. 1, n° 1, p. 82–89. [138](#)
- Leblond, C. et S. G. Reebs. 2006, «Individual leadership and boldness in shoals of golden shiners (*notemigonus crysoleucas*)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [127](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [127](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danio-*nin* fishes, including the zebrafish *danio rerio*», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [127](#)
- Miller, N. et R. Gerlai. 2012, «From schooling to shoaling : patterns of collective motion in zebrafish (*danio rerio*)», *PLoS One*, vol. 7, n° 11, p. e48865. [128](#)
- Miller, N. Y. et R. Gerlai. 2008, «Oscillations in shoal cohesion in zebrafish (*danio rerio*)», *Behavioural brain research*, vol. 193, n° 1, p. 148–151. [128](#)

- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [127](#)
- Parichy, D. M. 2015, «Advancing biology through a deeper understanding of zebrafish ecology and evolution», *ELife*, vol. 4, p. e05635. [127](#)
- Partridge, B. 1980, «The effect of school size on the structure and dynamics of minnow schools», *Animal Behaviour*, vol. 28, n° 1, p. 68–IN3. [139](#)
- Pérez-Escudero, A., J. Vicente-Page, R. C. Hinz, S. Arganda et G. G. de Polavieja. 2014, «idtracker : tracking individuals in a group by automatic identification of unmarked animals», *Nature methods*, vol. 11, n° 7, p. 743–748. [129](#)
- Peterson, R. O., A. K. Jacobs, T. D. Drummer, L. D. Mech et D. W. Smith. 2002, «Leadership behavior in relation to dominance and reproductive status in gray wolves, canis lupus», *Canadian Journal of Zoology*, vol. 80, n° 8, p. 1405–1412. [127](#)
- Pillot, M. H., J. Gautrais, J. Gouello, P. Michelena, R. Bon et collab.. 2010, «Moving together : Incidental leaders and naïve followers», *Behavioural Processes*, vol. 83, n° 3, p. 235–241. [127](#)
- Rands, S. A., G. Cowlshaw, R. A. Pettifor, J. M. Rowcliffe et R. A. Johnstone. 2003, «Spontaneous emergence of leaders and followers in foraging pairs», *Nature*, vol. 423, n° 6938, p. 432–434. [127](#)
- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, danio rerio», *Biological Reviews*, vol. 83, n° 1, p. 13–34. [127](#)
- Sueur, C., J.-L. Deneubourg, O. Petit et I. D. Couzin. 2010, «Differences in nutrient requirements imply a non-linear emergence of leaders in animal groups», *PLoS Comput Biol*, vol. 6, n° 9, p. e1000917. [127](#)
- Sueur, C. et O. Petit. 2008, «Shared or unshared consensus decision in macaques?», *Behavioural Processes*, vol. 78, n° 1, p. 84–92. [127](#)
- Ward, A. J., J. E. Herbert-Read, L. A. Jordan, R. James, J. Krause, Q. Ma, D. I. Rubenstein, D. J. Sumpter et L. J. Morrell. 2013, «Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish», *The American Naturalist*, vol. 181, n° 6, p. 748–760. [127](#), [138](#)
- Zienkiewicz, A., D. Barton, M. Porfiri et M. Di Bernardo. 2015, «Leadership emergence in a data-driven model of zebrafish shoals with speed modulation», *The European Physical Journal Special Topics*, vol. 224, n° 17-18, p. 3343–3360. [138](#)

Chapitre 8

Non periodic oscillation of AB strain zebrafish groups in a two-patch environment

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In prep.

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8.1 Résumé

Nous analysons l'utilisation de l'espace et les mouvements collectifs de groupes de 5 *Danio rerio* AB dans un système expérimental contraint de type deux chambres connectées par un couloir. Dans de précédentes publications, nous avons déjà décrit ce système expérimental similaire à des environnements fragmentés, dans lequel nous avons pu étudier le leadership et les transitions entre les chambres. Nous suivons les positions et les identités des poissons, affinons la notion de groupe et caractérisons précisément le temps passé dans chacune des zones par les poissons ainsi que les transitions collectives d'une chambre à l'autre. Tout d'abord, nous montrons que les zebrafish transitent collectivement, sans interruption, à travers le couloir. Nous remarquons aussi que ces transitions sont non périodiques. Enfin, l'occupation des chambres révèle qu'elle suit des règles mathématiques bien spécifiques, ce qui suggère une organisation non aléatoire des groupes de zebrafish.

8.2 Abstract

We explore for groups of 5 AB *Danio rerio* the utilisation of the space and the collective movements in a constrained set-up composed of two rooms connected by a corridor. We already described in few papers the set-up which is similar to a natural patchy environment. We track the positions and the identities of the fish, refine the notion of group, compute several metrics at the group level such as time spent in group in one of the three areas and characterize group transitions from a room to the other one. First, we show that zebrafish transit through the corridor without interruption, always in group. Second, these transitions are non-periodic for densities of 5 individuals. Third, the occupancy of the rooms by the groups follows specific mathematical laws suggesting a processed and non-random organisation of the groups of zebrafish.

8.3 Introduction

Among the animal collective behaviours, researchers have evidenced in many species collective movements [Bourjade et collab. \[2015\]](#); [Engeszer et collab. \[2007\]](#); [Hemelrijk et Hildenbrandt \[2012\]](#); [Herbert-Read et collab. \[2011\]](#); [Parrish et collab. \[2002\]](#); [Petit et Bon \[2010\]](#); [Radakov \[1973\]](#); [Sueur et collab. \[2011a,b\]](#), nest site selections [Amé et collab. \[2006\]](#); [Dahlbom et collab. \[2011\]](#); [Franks et collab. \[2002\]](#); [Rieucan et collab. \[2010\]](#) and site transitions [Bourjade et collab. \[2009\]](#); [Harcourt et collab. \[2009\]](#); [Leca et collab. \[2003\]](#); [Petit et collab. \[2009\]](#). The study of the transitions relies on decision-making processes and individual or collective preferences for environmental [Conradt et Roper \[2005\]](#)

or group members characteristics [Engeszer et collab. \[2007, 2004\]](#); [Hoare et collab. \[2004\]](#); [Pritchard et collab. \[2001\]](#).

In recent papers [Collignon et collab. \[2017\]](#); [Séguret et collab. \[2017, 2016\]](#), we have shown that *Danio rerio* (zebrafish) are always on the move whatever the type of environment (open field or constrained set-ups). Most of the time in group, they transit without interruption between the areas (landmarks or patches). Oscillations of group behaviours are still little studied. The closest study about oscillations of group behaviours was published by Miller et al. [Miller et Gerlai \[2008\]](#). The authors noticed that the shoal cohesion of zebrafish in open field fluctuates periodically and frequently : fish move closer and farther away from their neighbors. We wonder how the group behaviours can be impacted by the environment and what makes the choices of the groups so versatile and very dynamic. constrained environments are generally used to study individual and collective preferences. Several types of constrained environments already exist such as corridor type, Y-maze, T-maze, Plus-maze, etc. We are convinced that the simplest and the most refined set-up will be appropriate for addressing these issues. Unlike most of the constrained environments where the animals have to face between different alternatives, every areas of choice of our set-up are identical. Here, we are no interested in the intrinsic preferences of each zebrafish but rather in the dynamics of the choices of the whole group.

We investigate the oscillations of 12 groups of 5 AB zebrafish, swimming in a constrained environment : two identical squared rooms connected by a long corridor. Zebrafish are gregarious vertebrate model organisms [Norton et Bally-Cuif \[2010\]](#); [Oliveira \[2014\]](#) often used in behavioural studies. In the laboratory as much as in the nature, the zebrafish behave in groups [Engeszer et collab. \[2007\]](#); [McClure et collab. \[2006\]](#); [Séguret et collab. \[2016\]](#); [Spence et collab. \[2008\]](#). They come from India and live in small groups or in big shoals of several hundreds of fish depending on the region and the quality of the water (temperature, pH, saltiness) or the quality of the environment (human activity, predators, ...) [Parichy \[2015\]](#); [Pritchard et collab. \[2001\]](#); [Suriyampola et collab. \[2016\]](#). Zebrafish live in a wide variability of habitats [Arunachalam et collab. \[2013\]](#); [Suriyampola et collab. \[2016\]](#) : they are found in river channels, irrigation canals or beels with slow moving water. We based our experimental method on the observations of fish swimming in a constrained set-up evoking irrigation canals [Spence et collab. \[2006\]](#) and patchy environments [Wiens \[1976\]](#). This set-up has already been used to study collective departures, leadership and group cohesion [Collignon et collab. \[2017\]](#); [Séguret et collab. \[2016\]](#).

8.4 Methods

Fish and housing

We bred 600 AB strain laboratory wild-type zebrafish (*Danio rerio*) up to the adult stage and raised them under the same conditions in tanks of 3.5L by groups of 20 fish in a zebrafish aquatic housing system (ZebTEC rack from Tecniplast) that controls water quality and renews 10% of water in the system every hour. Zebrafish descended from AB zebrafish from different research institutes in Paris (Institut Curie and Institut du Cerveau et de la Moelle Épineière). AB zebrafish show zebra skin patterns and have short tail and fins. They measure about 3.5 cm long. All zebrafish used during the experiments were adults from 7 to 8 months of age. We kept fish under laboratory conditions : 27°C, 500µS salinity with a 10 :14 day :night light cycle, pH is maintained at 7.5 and nitrites (NO²⁻) are below 0.3 mg/L. Zebrafish are fed two times a day (Special Diets Services SDS-400 Scientific Fish Food).

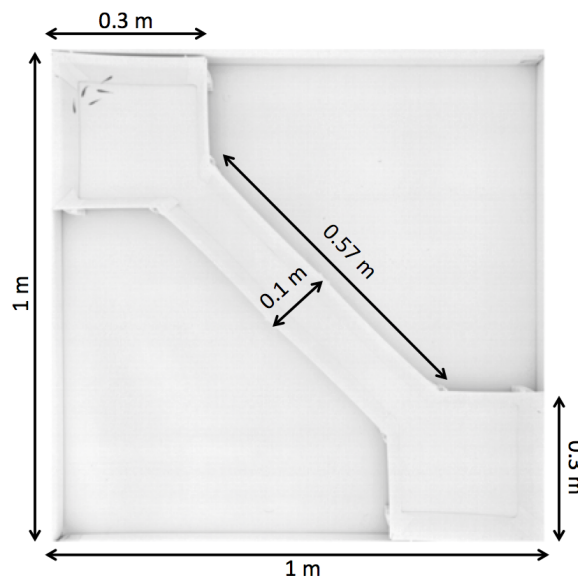


FIGURE 8.1 – **Experimental setup.** A tank of 1 m x 1 m is divided into three areas : two rooms (0.3 m x 0.3 m) connected by a corridor (0.57 m x 0.1 m). The water column has a height of 6 cm. The luminosity is ensured by 4 LED lamps of 33W (LP-500U) placed on corners of the tank and directed towards the walls to provide indirect lighting. The whole setup is confined in a 2 m x 2 m x 2.35 m experimental chamber surrounded by white sheets to isolate the experiments and to homogenise luminosity.

Experimental setup

The experimental tank consists in a 1.2 m x 1.2 m tank confined in a 2 m x 2 m x 2.35 m experimental area surrounded by white sheets, in order to isolate the experiments

and homogenise luminosity. A white opaque perspex frame (1 m x 1 m x 0.15 m - interior measures) is placed in the center of the tank. This frame help us to position the two rooms and the corridor. The squared rooms (0.3 m x 0.3 m) and the corridor (0.57 m x 0.1 m) have been designed on Computer-Aided Design (CAD) software and cut out from Poly(methyl methacrylate) (PMMA) plates of 0.003 m thickness. Each wall are tilted, (20° from the vertical) to the outside with a vertical height of 0.14 m, to avoid the presence of blind zones for the camera placed at the vertical of the tank. The water column has a height of 6 cm, the water pH is maintained at 7.5 and Nitrites (NO²⁻) are below 0.3 mg/L. The experiments were recorded by a high resolution camera (2048 px x 2048 px, Basler Scout acA2040-25gm) placed above the experimental tank and recording at 15 fps (frame per second). The luminosity is ensured by 4 LED lamps of 33W (LED LP-500U, colour temperature : 5500 K - 6000 K) placed on each corner of the tank, above the aquarium and directed towards the walls to provide indirect lightning.

Experimental procedure

We recorded the behaviour of zebrafish swimming in the setup during one hour and did 19 replicates with groups of 5 zebrafish. Every five replicates the setup was rotated by 90° to prevent potential environmental bias (noise, light, vibrations, ...). Before each replicate, the starting chamber, from which the fish are released, is chosen randomly. Then, the fish are placed with a hand net in a cylindrical arena (20 cm diameter) made of Plexiglas in the centre the selected rooms. Following a five minutes acclimatisation period, this cylinder is removed and the fish are free to swim in the setup. The fish were randomly selected regardless of their sex and each fish was never tested twice to prevent any form of learning.

Tracking & data analysis

Today, the studies on animal collective behaviours use methodologies based on massive data gathering, for exemple for flies (*Drosophila melanogaster*) [Branson et collab. \[2009\]](#); [Dankert et collab. \[2009\]](#), birds (*Sturnus vulgaris*) [Ballerini et collab. \[2008\]](#); [Miller et Gerlai \[2007, 2011\]](#), fish (*Notemigonus crysoleucas*) [Strandburg-Peshkin et collab. \[2013\]](#). Each replicate is tracked by post-processing ("off-line") with the idTracker software to identify each fish and their positions [Pérez-Escudero et collab. \[2014\]](#). Each replicate consists of 270000 positions. For a one hour video with 5 fish idTracker gives the results after 10 hours of processing (with a Dell Percision T5600, Processor : Two Intel Xeon Processor E5-2630 (Six Core, 2.30GHz Turbo, 15MB, 7.2 GT/s), Memory : 32GB (4x8GB) 1600MHz DDR3 ECC RDIMM).

Since idTracker solved collisions with accuracy we calculated individual measures and

characterised the aggregation level of the group.

We defined the majority events as the presence of more than 70% of the zebrafish, averaged on 1 second, in one of the three areas of the setup (either in the room 1 or in the room 2 or in the corridor) and as 4 fish minimum in one of the three areas including 1 fish possibly located in the corridor (or the room if the group is in the corridor) and going back in the room (or the corridor) with its conspecifics (non averaged on 1 second). In both cases, this operation guarantees that a majority event is ended by the departure of a fish and not by an error of detection during one frame by the tracking system. We then computed the durations of each of those events. All scripts were coded in Python using scientific and statistic libraries (numpy, pylab, scilab and matplotlib).

Statistics and calculations

For the Figures 8.3, we tested the distributions of the two methods that define the majority using Kolmogorov-Smirnov tests. For the Figure 8.4 we report the comparisons between the fits on the Table 8.1 and 8.2 of the annexe. These tests were made with the python package scipy. We chose 0.001 as significance level. We defined the autocorrelation as :

$$R_{ff}(\tau) = \int_{-\infty}^{+\infty} f(t)\bar{f}(t-\tau)dt \quad (8.1)$$

f is the signal which has to be analysed and \bar{f} its complex conjugate. Hence, we integrate the signal (the variations of the number of fish in each of the area) with itself in function of the lag τ . If there is a periodicity, we should have a periodic autocorrelated signal. The power spectral density (PSD) is defined as the Fourier transform of the autocorrelation. It shows the frequency distribution of the power of a signal according to the frequencies which compose it.

8.5 Results

8.5.1 Groups of zebrafish move continuously

In this paragraph we focus on the results of simple observations of 12 replicates with 5 AB zebrafish. The Figure 8.2, is an example of the dynamics of the transitions for one replicate. It shows that zebrafish swim generally in group and transit from one room to the other one. The dynamics of the transitions for the 19 replicates can found in the annexe (Figures 8.7, 8.8, 8.9, 8.10 and 8.11).

In the Figures 8.3 and 8.12 we see that the zebrafish spend short times in the rooms and the corridor.

In the Figures 8.4, 8.6 and Tables S 8.1 and S 8.2, we show different fitting methods of the distributions of the time occupancy of groups of zebrafish in both rooms. Both of

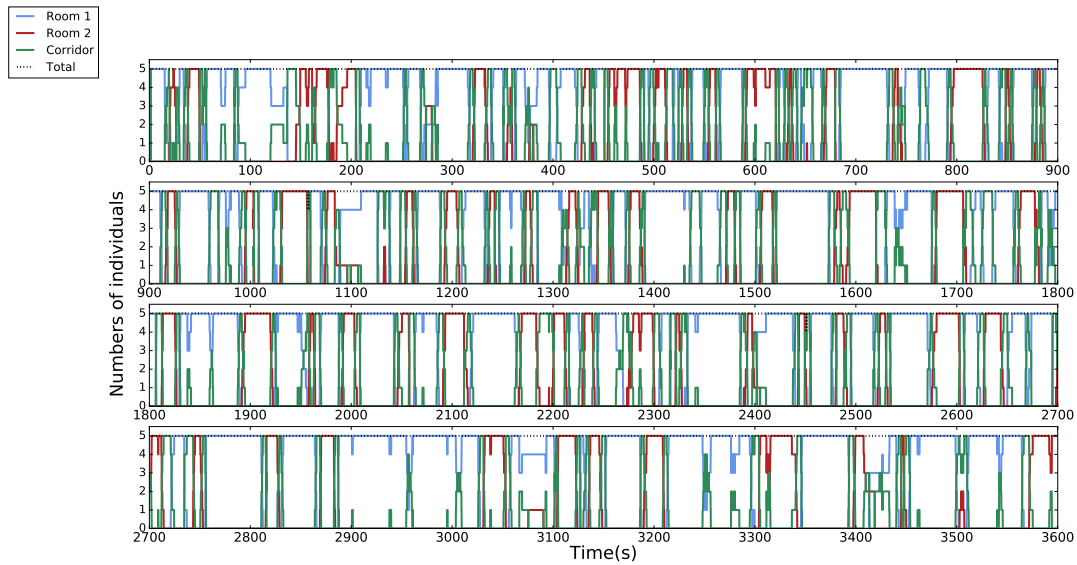


FIGURE 8.2 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for one replicate of one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

the histograms of the time occupancy in the rooms 1 and 2 (Figure 8.3) show that there is a regular structure. This is why we looked at different curve fitting methods. Our results strongly reject the hypothesis of power law and exponential fits (Tables 8.1 and 8.2). Also, they suggest that the best fitting method is the log-normal distribution or the troncated power law, without real preference for one or the other. As you can see, for each comparison of the fitting methods, the p – value is always low (< 0.003 or less), it means that the credibility ratio (R) is trustworthy.

8.5.2 Oscillations and collective departures

In the Figure 8.5 (A) we show an example of the autocorrelation of the dynamics of the transitions for one replicate. The autocorrelations for all the replicates are in the Annexe (Figures 8.13, 8.15 and 8.17). All these figures show the same tendency : there is no periodicity in the oscillations of the groups between the rooms. The Figure 8.5 (B) shows the Power Spectral Density (PSD) related to (A). The PSD for all the replicates are in the Annexe (Figures 8.14, 8.16 and 8.18). No peak of frequency stands out from all these figures.

Distributions	Log Normal		Exponential		Truncated Power Law	
	R	p	R	p	R	p
Power Law	-5.018	0.00	-0.992	0.32	-5.620	0.00
Truncated Power Law	2.701	0.01	3.267	0.00		
Exponential	-2.745	0.01				

Distributions	Power Law		Log Normal			Exponential		Truncated Power Law		
Parameters +	α	$t_{min}(s)$	μ	σ	$t_{min}(s)$	λ	$t_{min}(s)$	α	λ	$t_{min}(s)$
x_{min}	2.61	8.0	1.77	0.90	8.0	0.11	8.0	1.36	0.05	8.0

TABLEAU 8.1 – Table of the comparisons between different fits of the distributions of the time occupancy in the room 1 with power law, truncated power law, log-normal and exponential. This table is related to the Figure 8.3.

Distributions	Log Normal		Exponential		Truncated Power Law	
	R	p	R	p	R	p
Power Law	-5.804	0.00	-2.822	0.00	-5.332	0.00
Truncated Power Law	2.786	0.00	2.101	0.03		
Exponential	-1.134	0.26				

Distributions	Power Law		Log Normal			Exponential		Truncated Power Law		
Parameters +	α	$t_{min}(s)$	μ	σ	$t_{min}(s)$	λ	$t_{min}(s)$	α	λ	$t_{min}(s)$
x_{min}	2.66	8.0	1.97	0.80	8.0	0.11	8.0	1.03	0.07	8.0

TABLEAU 8.2 – Table of the comparisons between different fits of the distributions of the time occupancy in the room 2 with power law, truncated power law, log-normal and exponential. This table is related to the Figure 8.3.

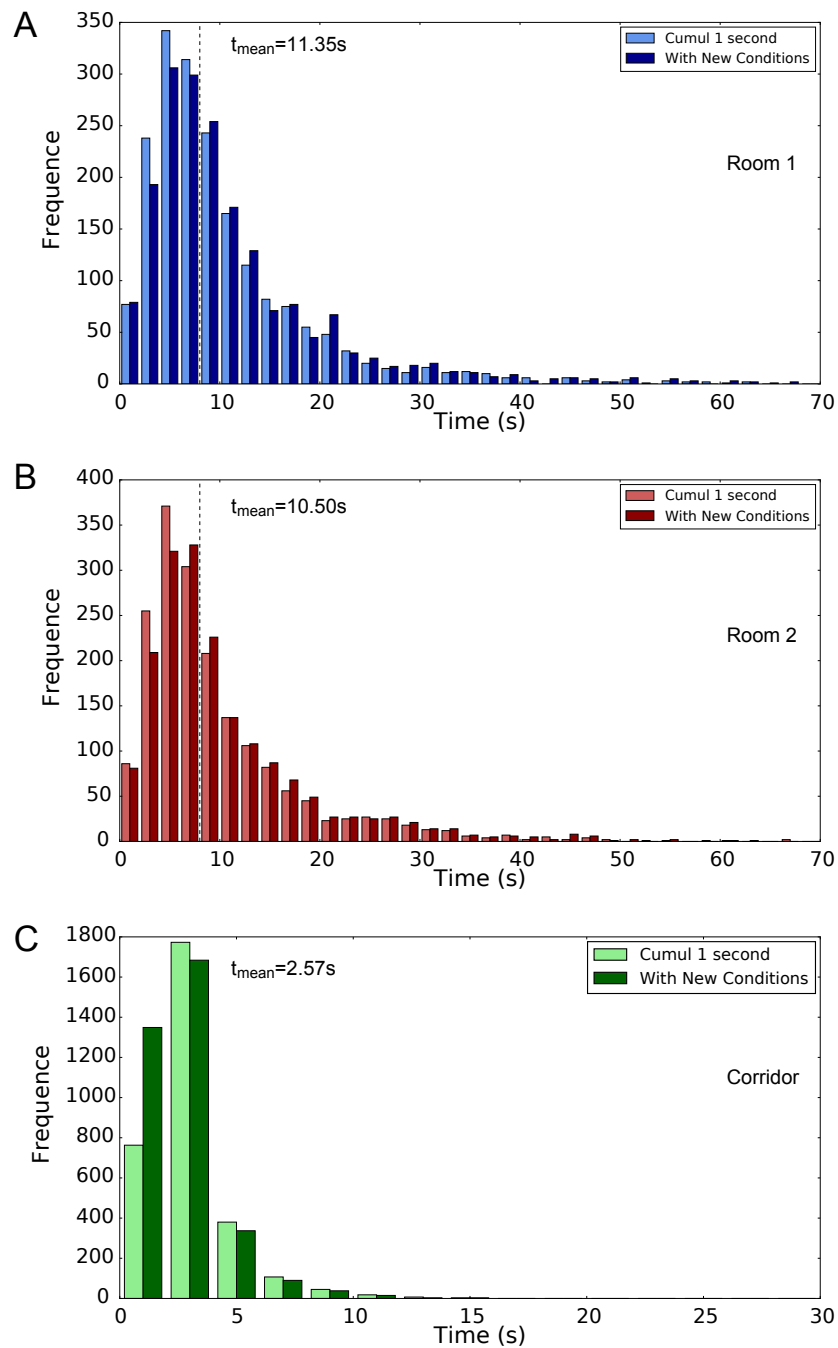


FIGURE 8.3 – **Time occupancy of groups of zebrafish** (A) in the room 1, (B) in the room 2 and (C) in the corridor. They stay few seconds in the corridor (mean = 2.57 s) as in both of the rooms (in the room 1, mean = 11.35 s and in the room 2, mean = 10.50 s).

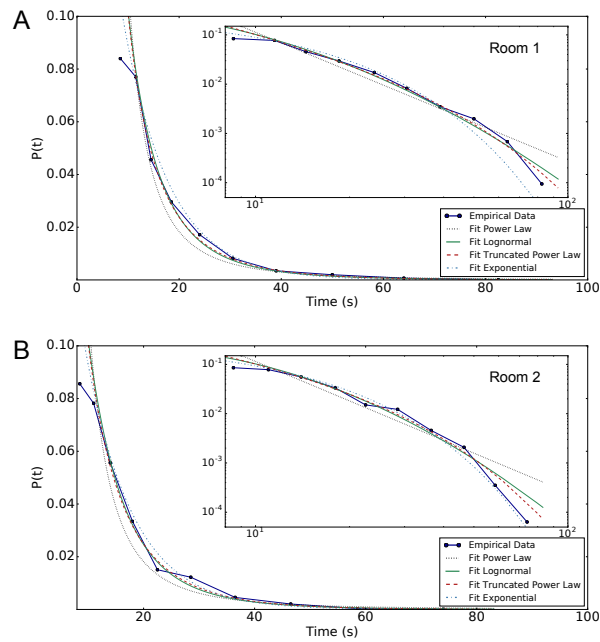


FIGURE 8.4 – **Fits of time occupancy of groups of zebrafish** (A) in the room 1 and (B) in the room 2. The best fits for the time occupancy distributions in both rooms are the log-normal distribution and the troncated power law (see Table S 8.1 and S 8.2).

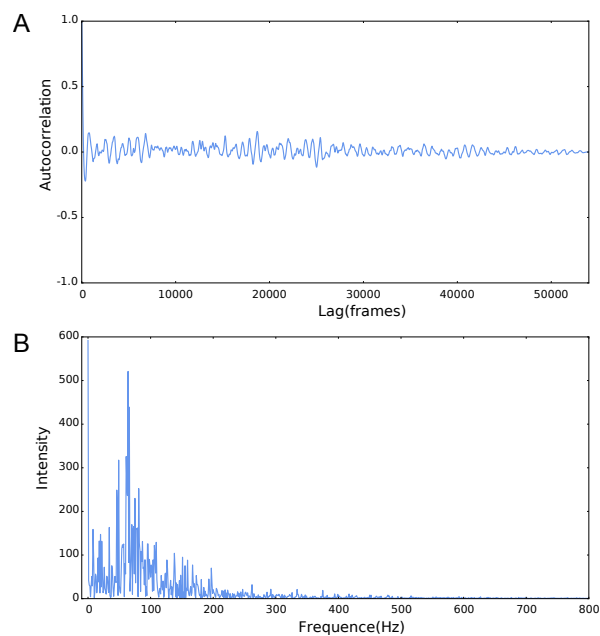


FIGURE 8.5 – **Non periodic oscillations between the rooms.** (A) Example of the autocorrelation of the dynamics of the transitions for one replicate of one hour with 5 AB zebrafish, focused on the room 1. The values fluctuate around 0 and show no periodicity. (B) Example of the Power Spectral Density (PSD) related to the previous autocorrelation. No frequency peak is highlighted.

8.6 Discussion

We studied the transitions and the oscillations of group movements of AB zebrafish between two patches (rooms) connected by a corridor. We improved the methodology of the characterisation of the majority of the group. In a previous paper [Séguret et collab. \[2016\]](#), we defined the majority as 70% of the whole population at each second. In this paper, we refine the majority as 4 fish minimum in one of the three areas including 1 fish possibly located in the corridor (or the room if the group is in the corridor) and going back in the room (or corridor) with its conspecifics (non averaged on 1 second). Through this computation, we managed to decrease false positives for short durations of occupancy in both rooms. We made a Kolmogorov-Smirnov test to compare the distributions with the two methods of computation of the majority. For all areas, the distributions of both methods of computation are significantly different : in the room 1, $p - value < 0.001, D = 0.114$; in the room 2, $p - value < 0.001, D = 0.138$; in the corridor, $p - value < 0.001, D = 0.198$. The results of the [Figure 8.3](#) strongly show that in the rooms (A and B) and in the corridor (C), fish spend very short time. These results combined with those from the [figure 8.2](#) confirm that zebrafish travel together, are always on the move and transit without interruption between the patches. Incidentally, [Miller et al. Miller et Gerlai \[2008\]](#) have shown that shoal density of zebrafish fluctuate periodically (around 20 seconds). On one hand, this observation confirm what we described above : zebrafish stay generally in group. On the other hand, we wondered if these periodic oscillations that go along with the structure of the shoal could be also found in the displacement of the shoal. In other species, [Cole \[1991\] Cole and Boi et collab. \[1999\] Boi et al.](#), have shown that the activity levels of ant colonies are periodic. For *Leptothorax allardycei*, they found a cycle activity around 26 minutes and for *Leptothorax acervorum*, it was around 20 minutes. Thinking further, we find in the literature other types of periodic events : [Leinaas, Leinaas \[1983\]](#) with *Collembola Hypogastrura* and [Fowler et al., Fowler et Gobbi \[1988\]](#) with *Eriophora bistrata* have shown periodic cycles and synchronisation of moulting.

This is why we characterised the oscillations of groups of zebrafish swimming from a room to the other one. However we show that they are non periodic ([Figure 8.5](#)). [Collignon et al. Collignon et collab. \[2017\]](#) show that leadership of zebrafish is generally shared between all the members of the shoal and that a transition from a patch to another one is always initiated by one individual (a temporary leader). Our observation strengthens the idea that groups of zebrafish need leaders. Actually, if leadership was not essential for the group in making the decisions, we suggest that the oscillations between the patches would have been periodic.

8.7 Supplementary information and figures

Supplementary figures of "Non periodic oscillation of AB strain zebrafish groups in a two-patch environment".

8.7.1 Oscillations and collective departures

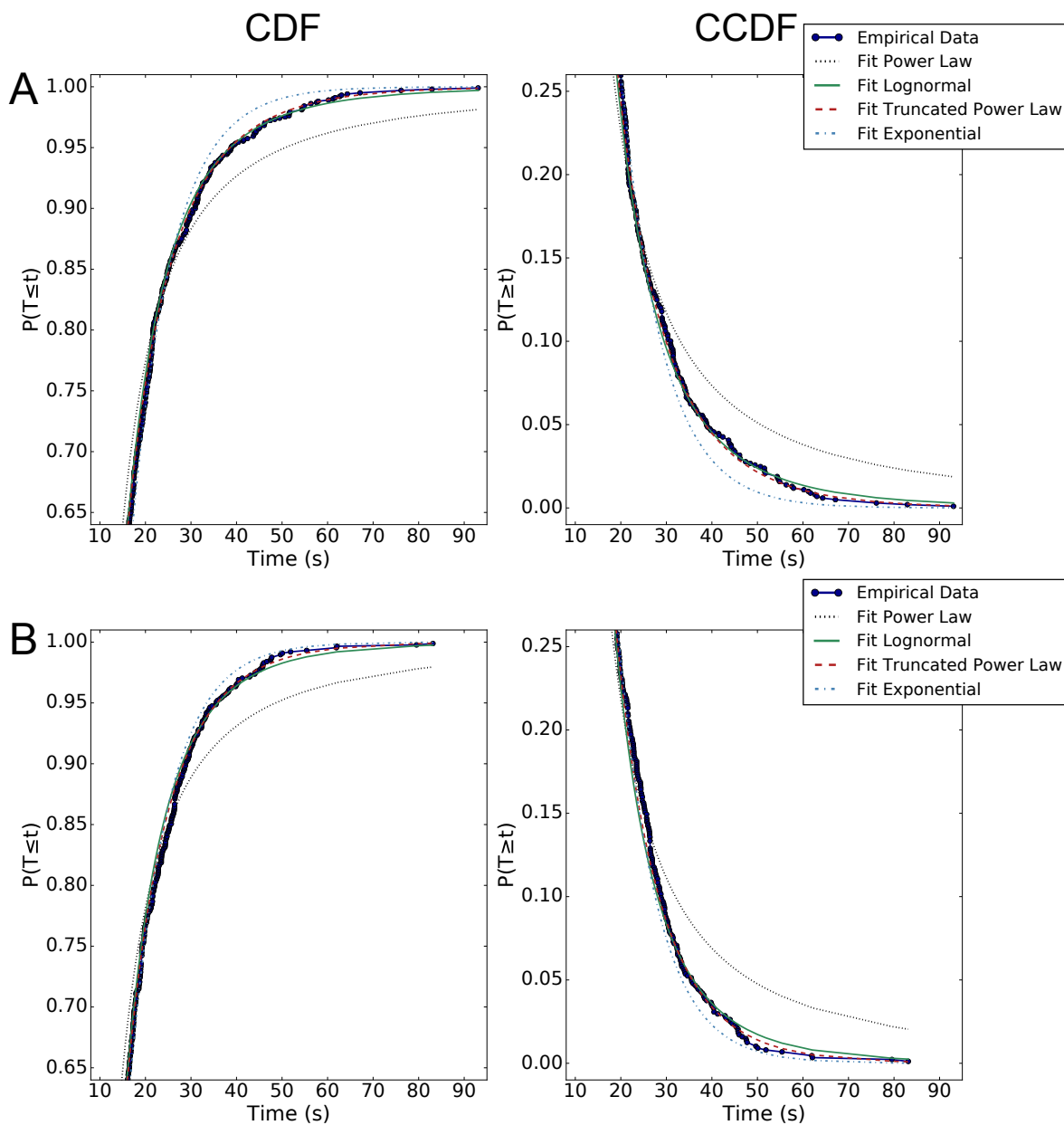


FIGURE 8.6 – Cumulative distribution functions (CDF) and complementary cumulative distribution functions (CCDF) of the time occupancy of groups of zebrafish (A) in the room 1 and (B) in the room 2.

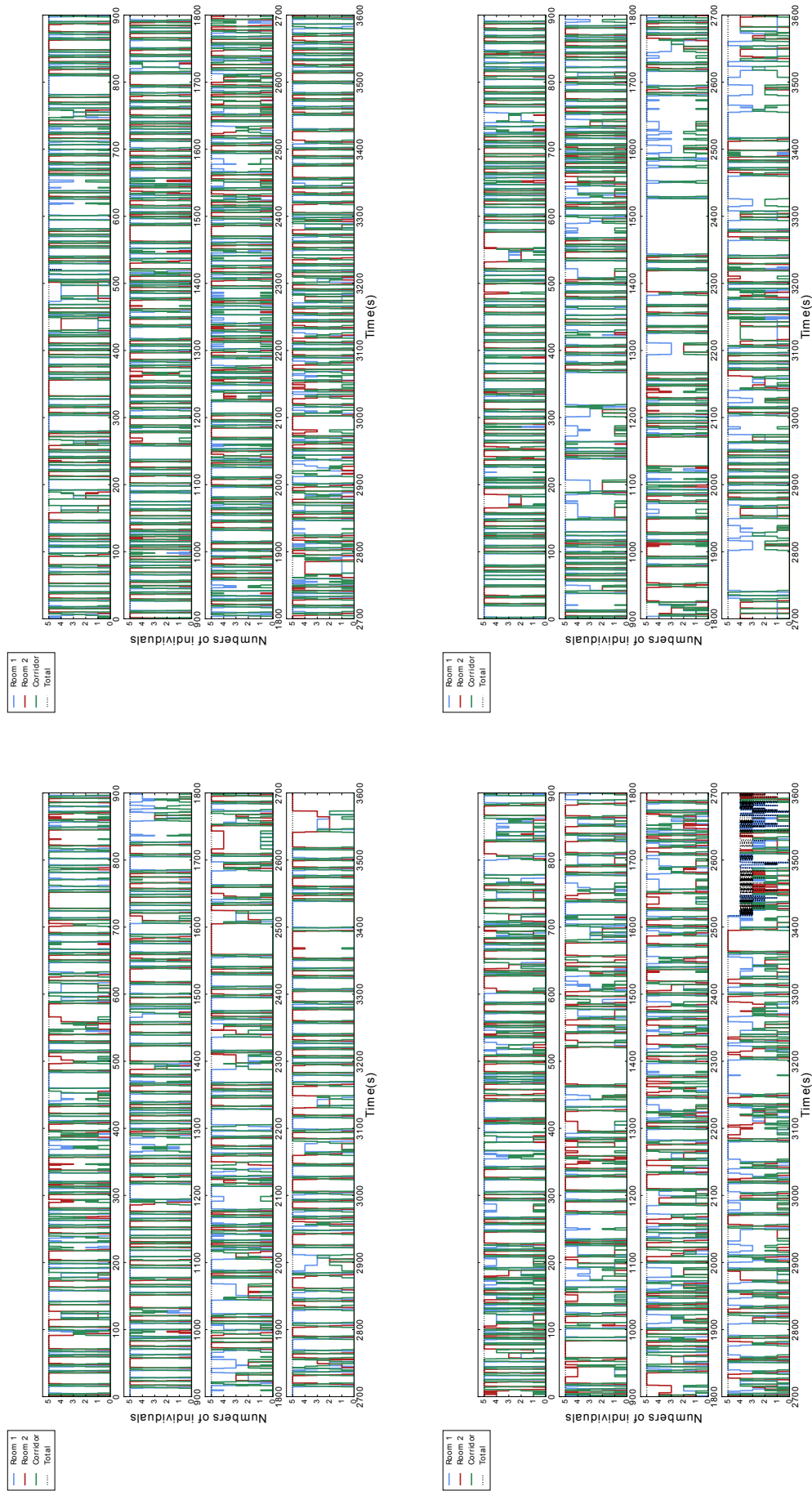


FIGURE 8.7 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for a replicated one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

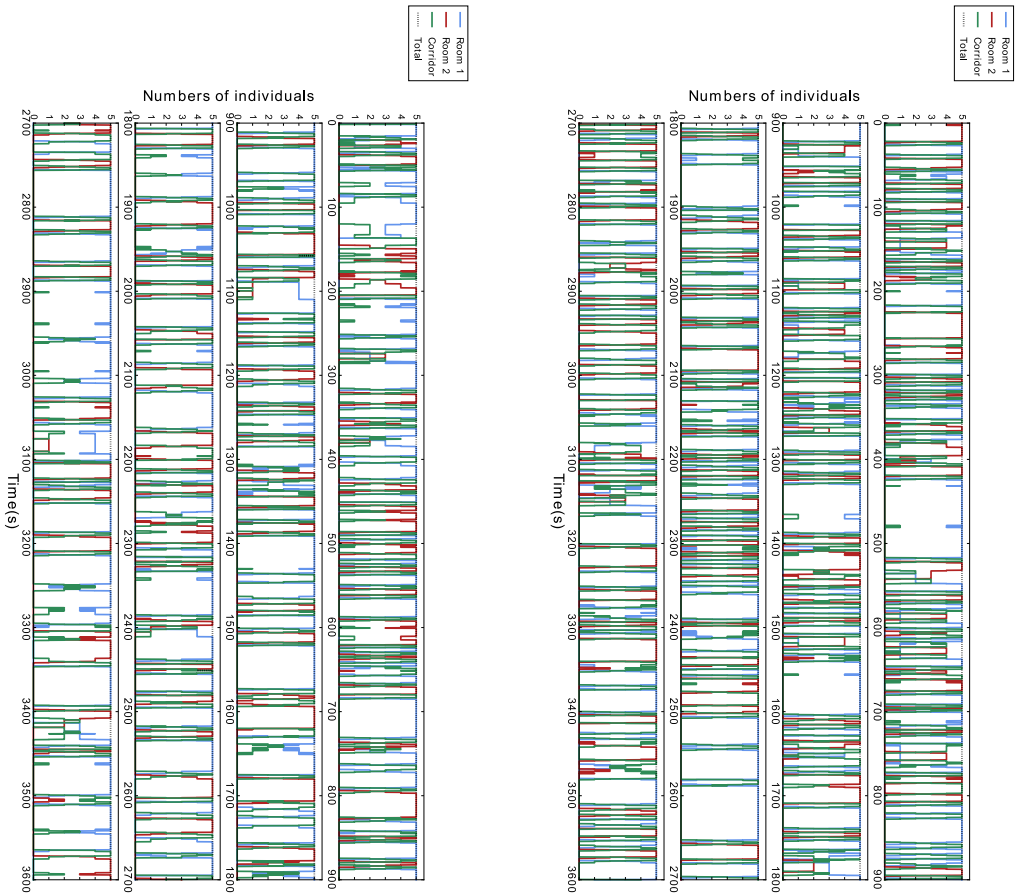


FIGURE 8.8 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for a replicated of one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

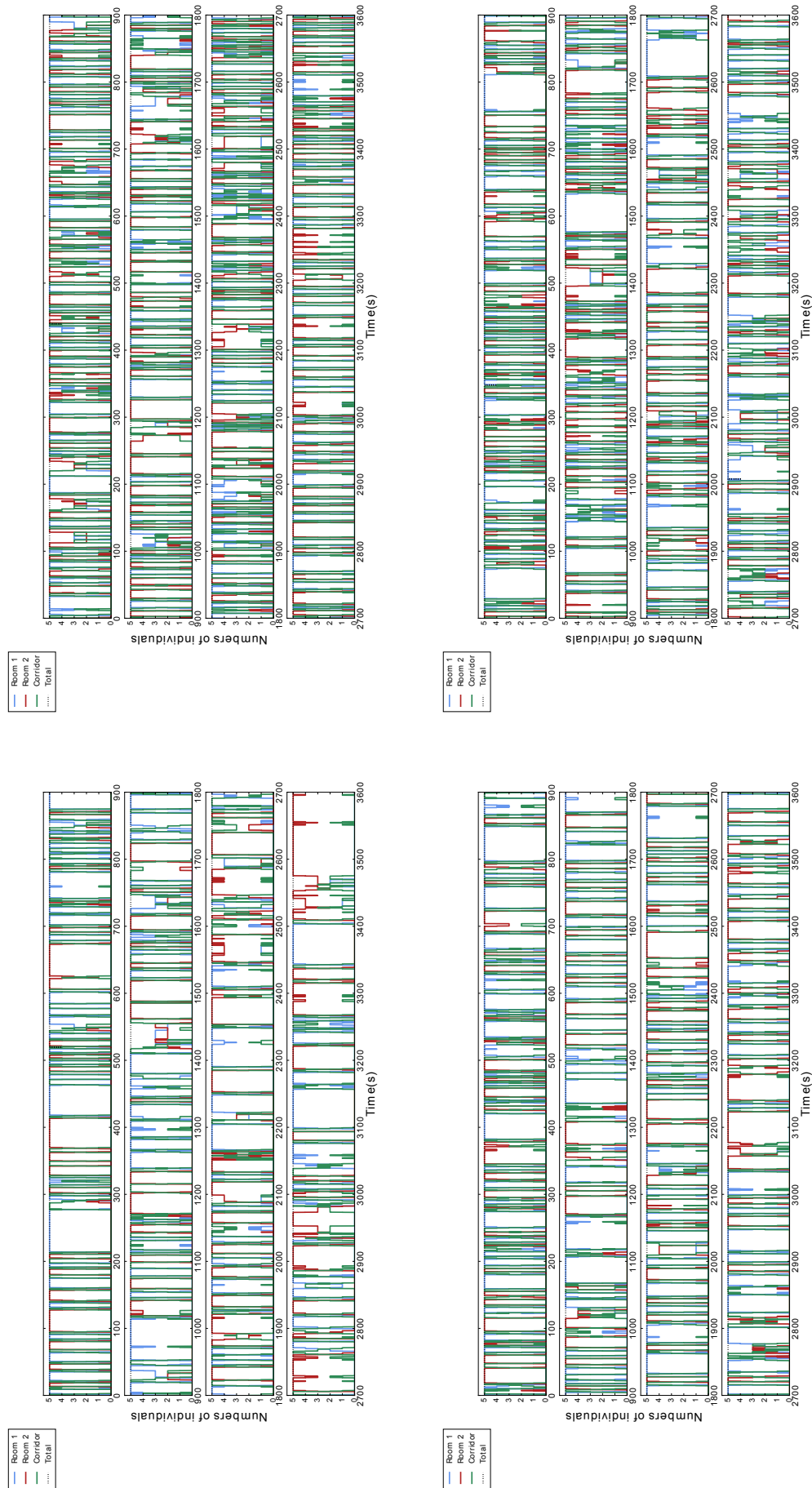


FIGURE 8.9 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for a replicated one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

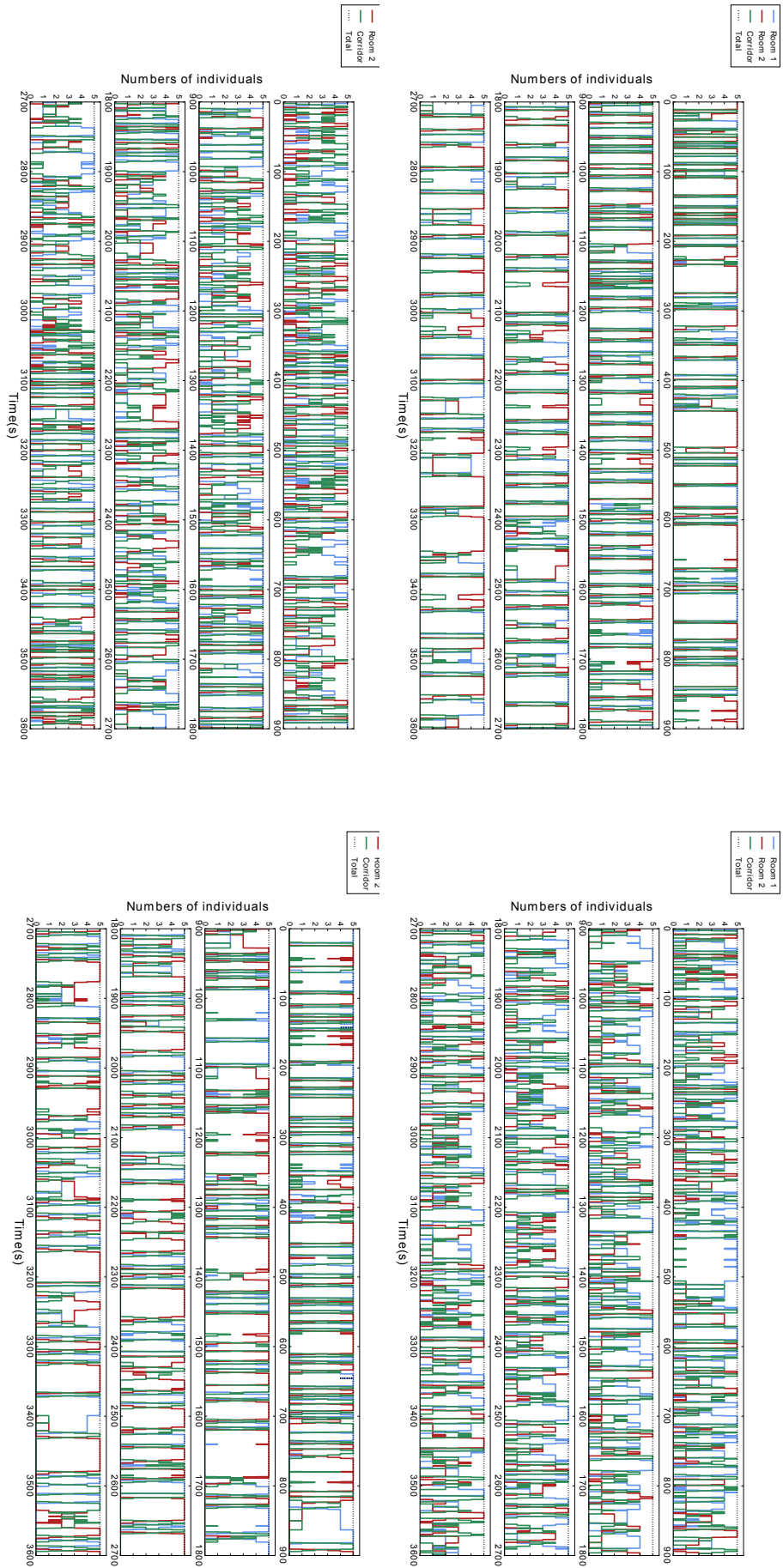


FIGURE 8.10 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for a replicated of one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

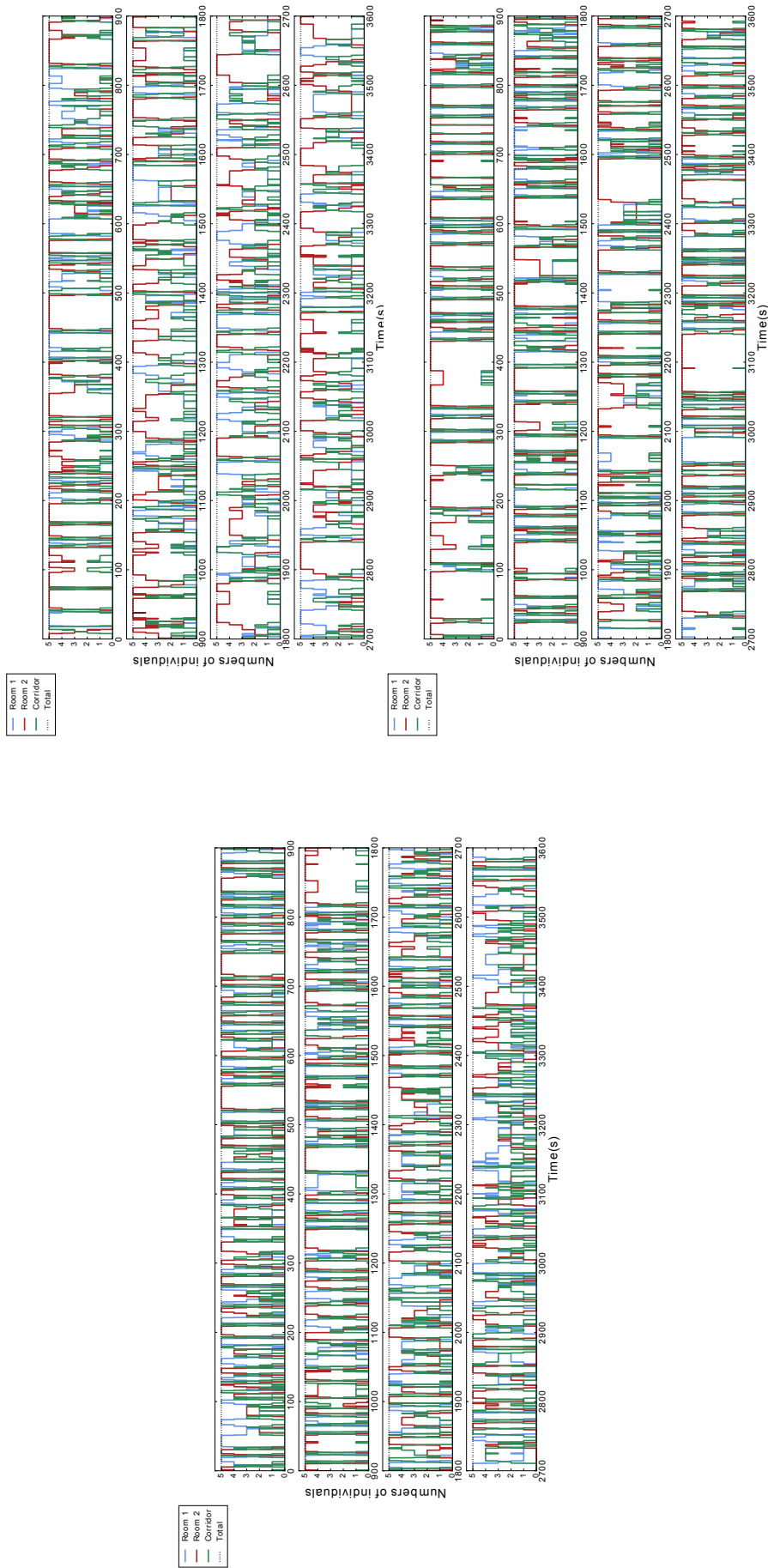


FIGURE 8.11 – **The zebrafish transit between the rooms.** Example of the dynamics of the transitions for a replicated of one hour with 5 AB zebrafish. In blue the number of fish in the room 1, in red the room 2, in green the corridor and the black broken line for the sum of the whole population.

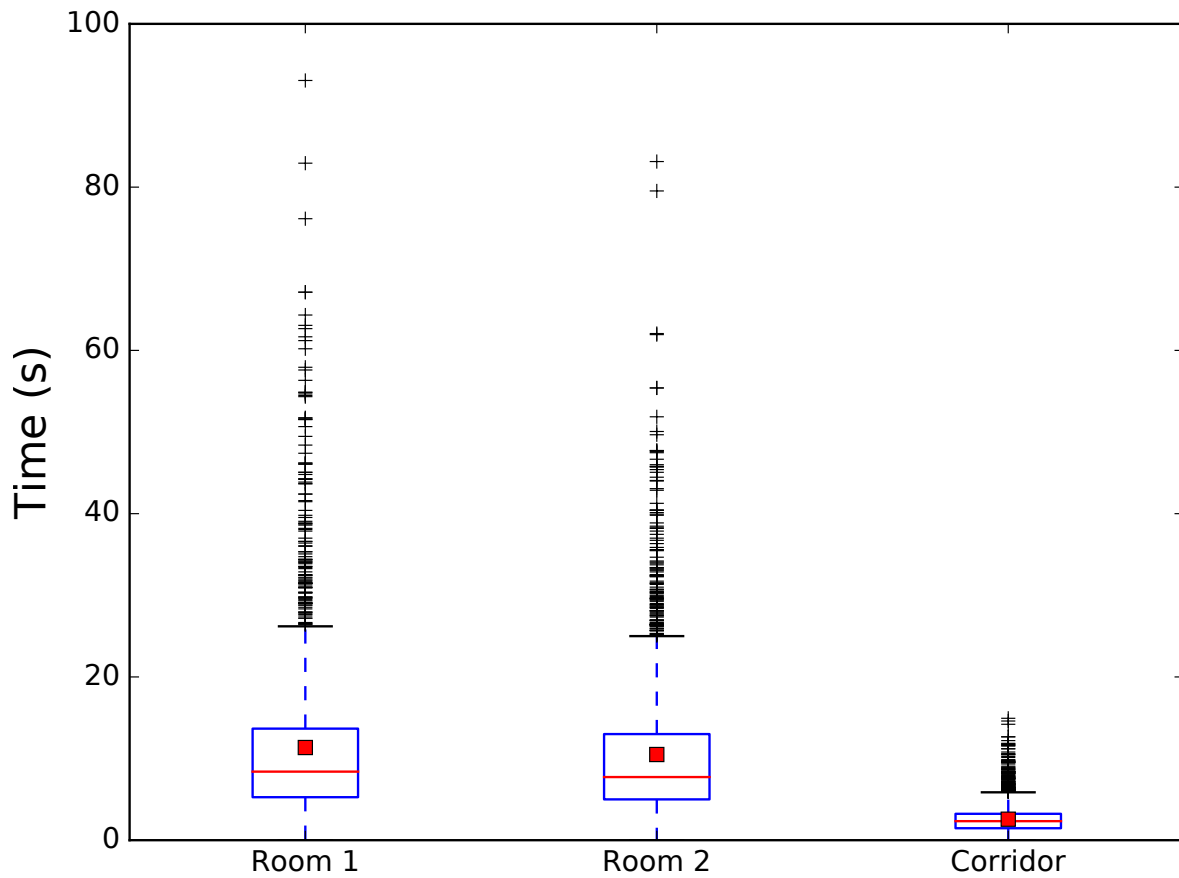


FIGURE 8.12 – Distributions of time of majority in the rooms and the corridor for 19 replicates. The red line shows the median and the red square is the mean. * = p -value < 0.05, ** = p -value < 0.01, *** = p -value < 0.001, ns = non significant.

8.7.2 Oscillations and collective departures

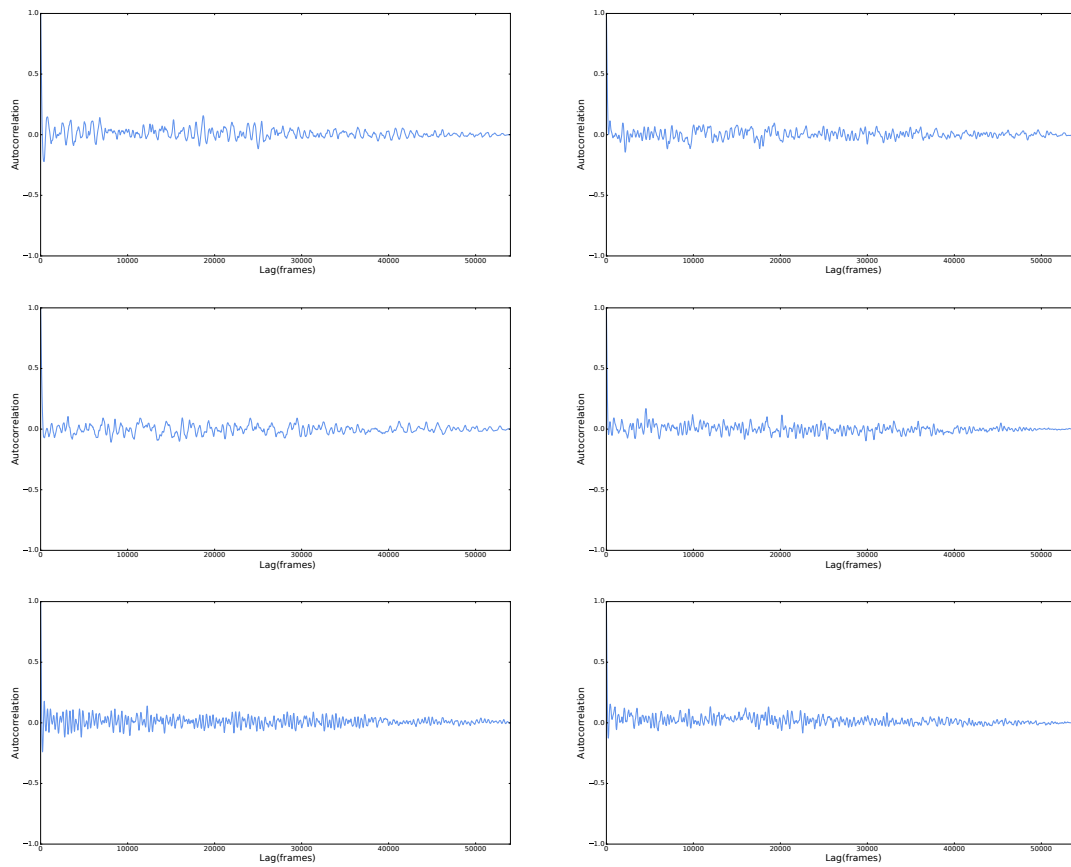


FIGURE 8.13 – **Autocorrelations of the dynamics of the transitions** for six replicates of one hour with 5 AB zebrafish, focused on the room 1.

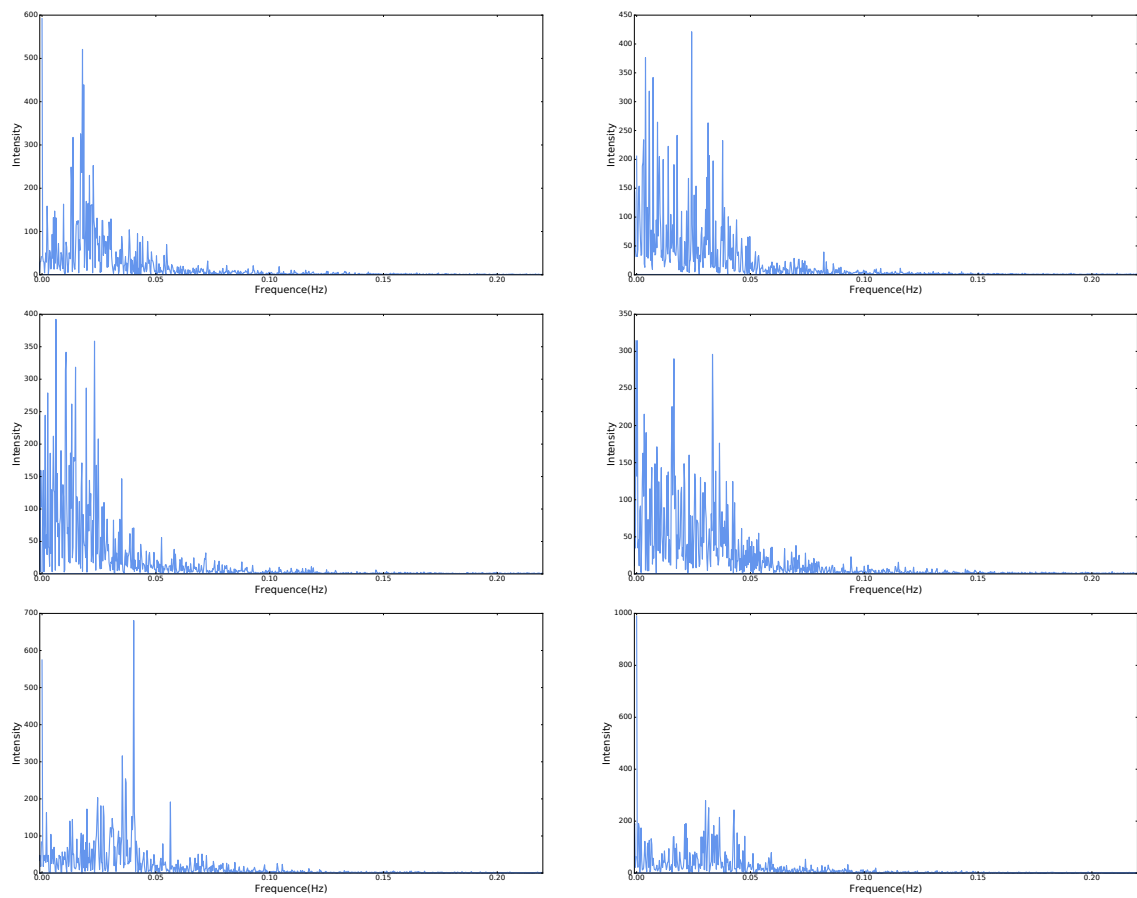


FIGURE 8.14 – **Power Spectral Density (PSD)** related to the previous autocorrelations.

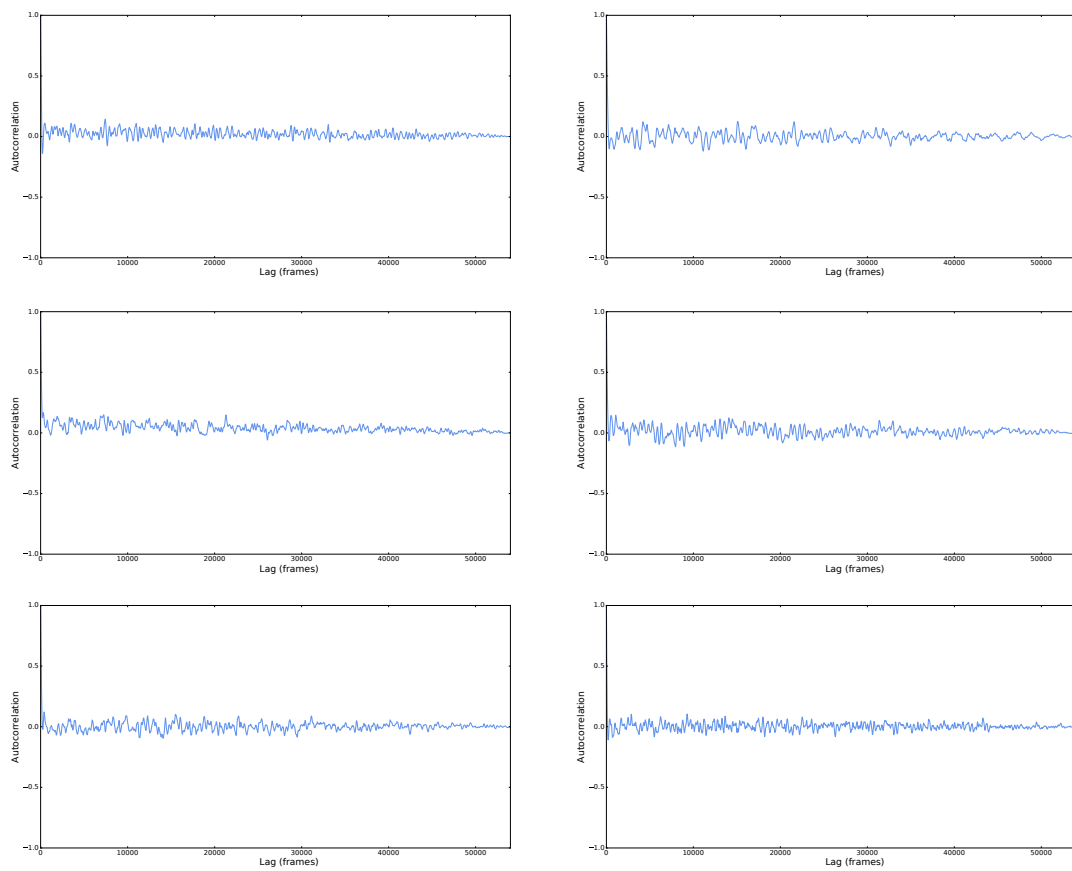


FIGURE 8.15 – Autocorrelations of the dynamics of the transitions for six replicates of one hour with 5 AB zebrafish, focused on the room 1.

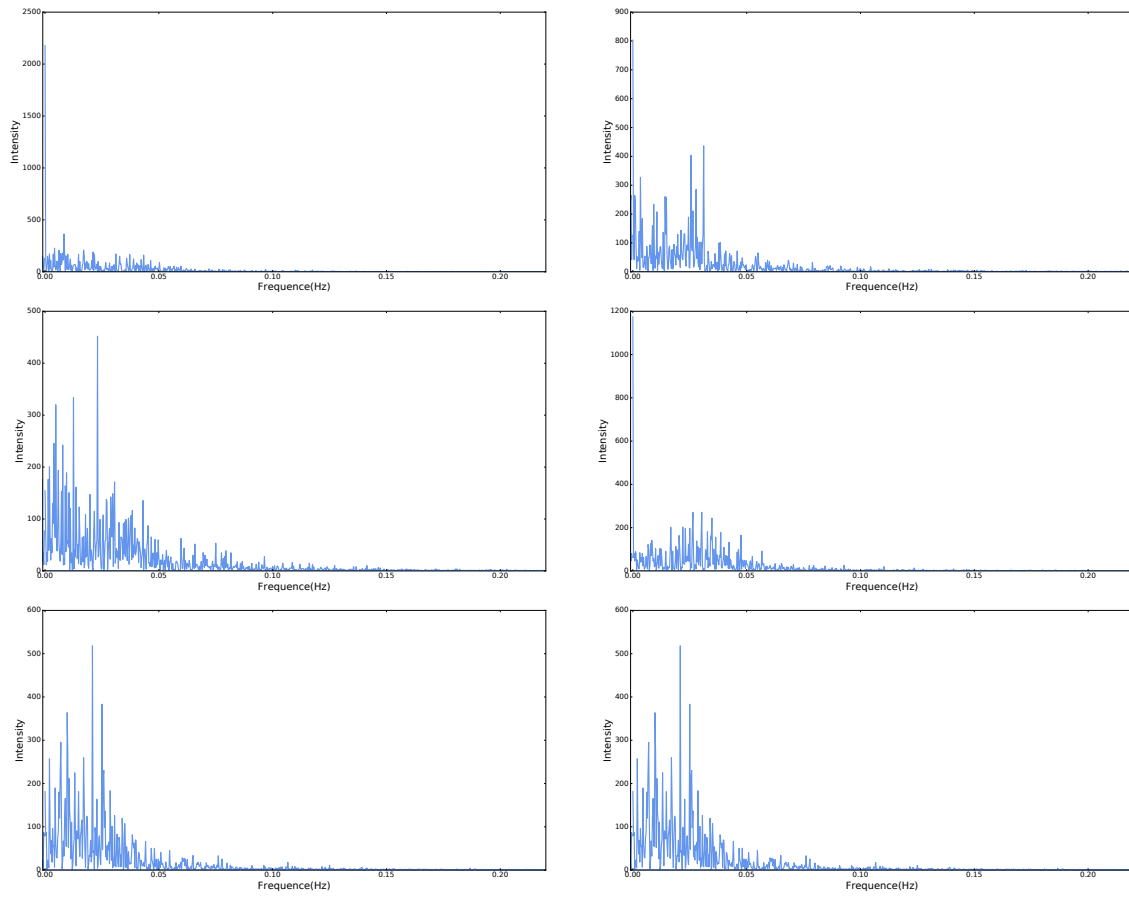


FIGURE 8.16 – **Power Spectral Density (PSD)** related to the previous autocorrelations.

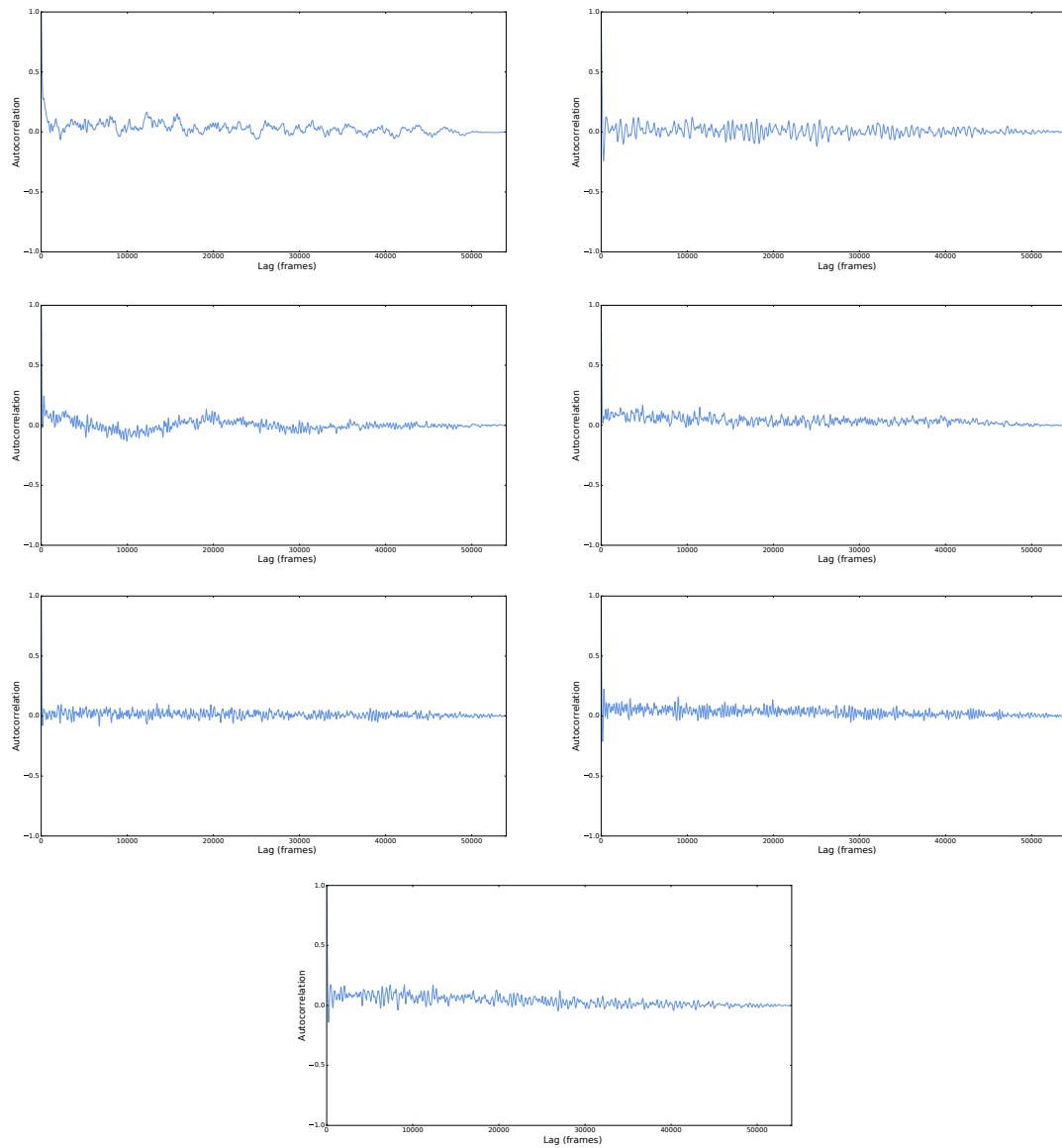


FIGURE 8.17 – **Autocorrelations of the dynamics of the transitions** for seven replicates of one hour with 5 AB zebrafish, focused on the room 1.

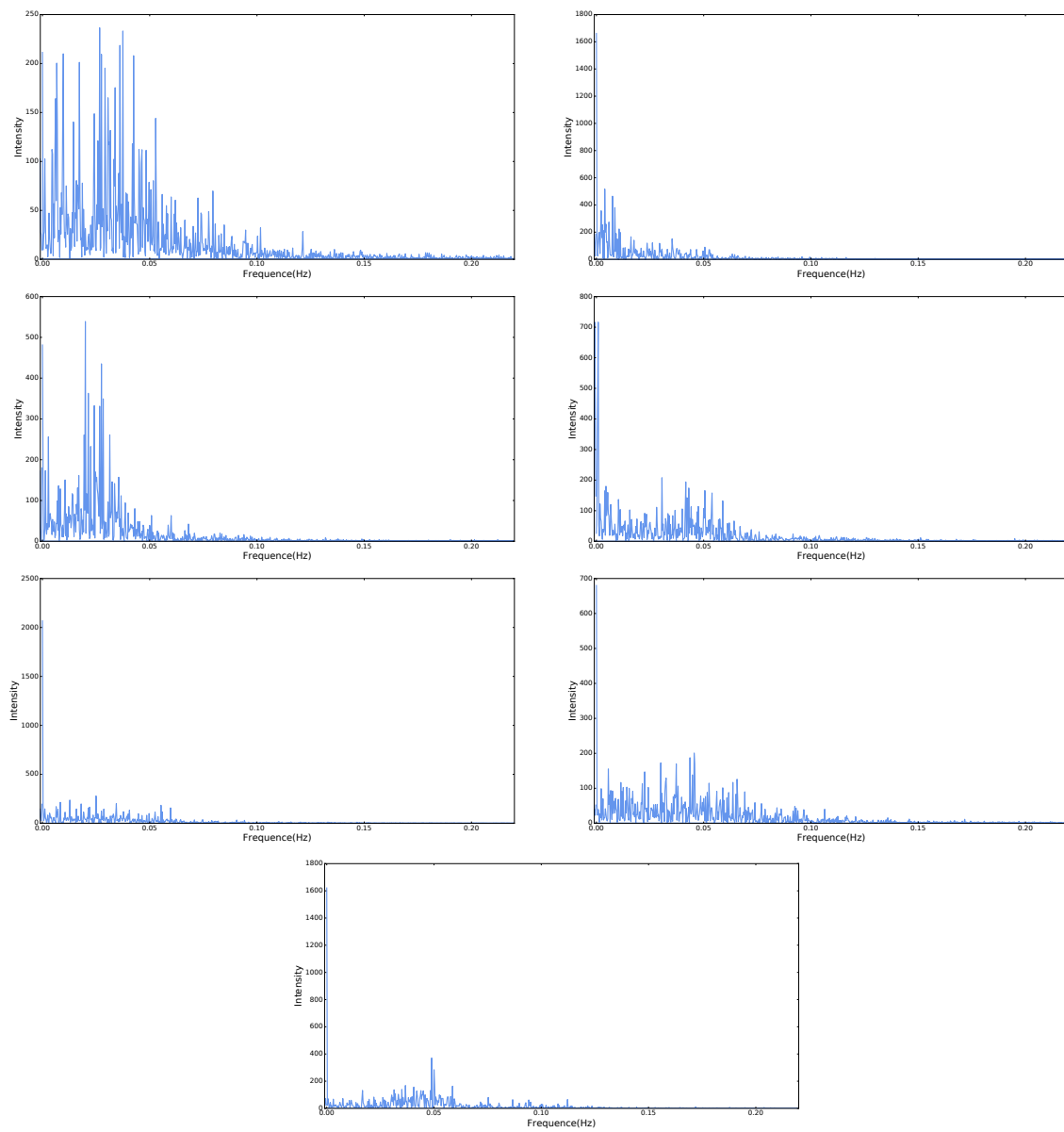


FIGURE 8.18 – **Power Spectral Density (PSD)** related to the previous autocorrelations.

8.8 Références

- Amé, J.-M., J. Halloy, C. Rivault, C. Detrain et J. L. Deneubourg. 2006, «Collegial decision making based on social amplification leads to optimal group formation», *Proceedings of the National Academy of Sciences*, vol. 103, n° 15, p. 5835–5840. [144](#)
- Arunachalam, M., M. Raja, C. Vijayakumar, P. Malaiammal et R. L. Mayden. 2013, «Natural history of zebrafish (*danio rerio*) in india», *Zebrafish*, vol. 10, n° 1, p. 1–14. [145](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini et collab.. 2008, «Interaction ruling animal collective behavior depends on topological rather than metric distance : Evidence from a field study», *Proceedings of the national academy of sciences*, vol. 105, n° 4, p. 1232–1237. [147](#)
- Boi, S., I. Couzin, N. Del Buono, N. Franks et N. Britton. 1999, «Coupled oscillators and activity waves in ant colonies», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 266, n° 1417, p. 371–378. [153](#)
- Bourjade, M., B. Thierry, M. Hausberger et O. Petit. 2015, «Is leadership a reliable concept in animals? an empirical study in the horse», *PloS one*, vol. 10, n° 5, p. e0126344. [144](#)
- Bourjade, M., B. Thierry, M. Maumy et O. Petit. 2009, «Decision-making in przewalski horses (*equus ferus przewalskii*) is driven by the ecological contexts of collective movements», *Ethology*, vol. 115, n° 4, p. 321–330. [144](#)
- Branson, K., A. A. Robie, J. Bender, P. Perona et M. H. Dickinson. 2009, «High-throughput ethomics in large groups of drosophila», *Nature methods*, vol. 6, n° 6, p. 451–457. [147](#)
- Cole, B. J. 1991, «Short-term activity cycles in ants : generation of periodicity by worker interaction», *The American Naturalist*, vol. 137, n° 2, p. 244–259. [153](#)
- Collignon, B., A. Séguret, Y. Chemtob, L. Cazenille et J. Halloy. 2017, «Collective departures in zebrafish : profiling the initiators», *arXiv preprint arXiv :1701.03611*. [145](#), [153](#)
- Conradt, L. et T. J. Roper. 2005, «Consensus decision making in animals», *Trends in ecology & evolution*, vol. 20, n° 8, p. 449–456. [144](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [144](#)
- Dankert, H., L. Wang, E. D. Hoopfer, D. J. Anderson et P. Perona. 2009, «Automated monitoring and analysis of social behavior in drosophila», *Nature methods*, vol. 6, n° 4, p. 297–303. [147](#)
- Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan et D. M. Parichy. 2007, «Timing and plasticity of shoaling behaviour in the zebrafish, *danio rerio*», *Animal behaviour*, vol. 74, n° 5, p. 1269–1275. [144](#), [145](#)

- Engeszer, R. E., M. J. Ryan et D. M. Parichy. 2004, «Learned social preference in zebrafish», *Current Biology*, vol. 14, n° 10, p. 881–884. [145](#)
- Fowler, H. et N. Gobbi. 1988, «Communication and synchronized molting in a colonial araneid spider, *Eriophora bistriata*», *Cellular and Molecular Life Sciences*, vol. 44, n° 8, p. 720–722. [153](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [144](#)
- Harcourt, J. L., T. Z. Ang, G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Social feedback and the emergence of leaders and followers», *Current Biology*, vol. 19, n° 3, p. 248–252. [144](#)
- Hemelrijk, C. K. et H. Hildenbrandt. 2012, «Schools of fish and flocks of birds : their shape and internal structure by self-organization», *Interface focus*, p. rsfs20120025. [144](#)
- Herbert-Read, J. E., A. Perna, R. P. Mann, T. M. Schaerf, D. J. Sumpter et A. J. Ward. 2011, «Inferring the rules of interaction of shoaling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18726–18731. [144](#)
- Hoare, D., I. D. Couzin, J.-G. Godin et J. Krause. 2004, «Context-dependent group size choice in fish», *Animal Behaviour*, vol. 67, n° 1, p. 155–164. [145](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [144](#)
- Leinaas, H. P. 1983, «Synchronized moulting controlled by communication in group-living collembola», *Science*, vol. 219, n° 4581, p. 193–195. [153](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danio-nin fishes, including the zebrafish *Danio rerio*», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [145](#)
- Miller, N. et R. Gerlai. 2007, «Quantification of shoaling behaviour in zebrafish (*Danio rerio*)», *Behavioural brain research*, vol. 184, n° 2, p. 157–166. [147](#)
- Miller, N. Y. et R. Gerlai. 2008, «Oscillations in shoal cohesion in zebrafish (*Danio rerio*)», *Behavioural brain research*, vol. 193, n° 1, p. 148–151. [145](#), [153](#)
- Miller, N. Y. et R. Gerlai. 2011, «Shoaling in zebrafish : what we don't know», *Reviews in the Neurosciences*, vol. 22, n° 1, p. 17–25. [147](#)
- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [145](#)
- Oliveira, R. F. 2014, «Mind the fish : zebrafish as a model in cognitive social neuroscience», *Frontiers in neural circuits*. [145](#)

- Parichy, D. M. 2015, «Advancing biology through a deeper understanding of zebrafish ecology and evolution», *ELife*, vol. 4, p. e05635. [145](#)
- Parrish, J. K., S. V. Viscido et D. Grünbaum. 2002, «Self-organized fish schools : an examination of emergent properties», *The biological bulletin*, vol. 202, n° 3, p. 296–305. [144](#)
- Pérez-Escudero, A., J. Vicente-Page, R. C. Hinz, S. Arganda et G. G. de Polavieja. 2014, «idtracker : tracking individuals in a group by automatic identification of unmarked animals», *Nature methods*, vol. 11, n° 7, p. 743–748. [147](#)
- Petit, O. et R. Bon. 2010, «Decision-making processes : the case of collective movements», *Behavioural Processes*, vol. 84, n° 3, p. 635–647. [144](#)
- Petit, O., J. Gautrais, J.-B. Leca, G. Theraulaz et J.-L. Deneubourg. 2009, «Collective decision-making in white-faced capuchin monkeys», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1672, p. 3495–3503. [144](#)
- Pritchard, V. L., J. Lawrence, R. K. Butlin et J. Krause. 2001, «Shoal choice in zebrafish, danio rerio : the influence of shoal size and activity», *Animal Behaviour*, vol. 62, n° 6, p. 1085–1088. [145](#)
- Radakov, D. V. 1973, «Schooling in the ecology of fish», . [144](#)
- Rieucou, G., J. Morand-Ferron et L.-A. Giraldeau. 2010, «Group size effect in nutmeg mannikin : between-individuals behavioral differences but same plasticity», *Behavioral Ecology*, p. arq039. [144](#)
- Séguret, A., B. Collignon, L. Cazenille, Y. Chemtob et J. Halloy. 2017, «Loose social organisation of ab strain zebrafish groups in a two-patch environment», *arXiv preprint arXiv :1701.02572*. [145](#)
- Séguret, A., B. Collignon et J. Halloy. 2016, «Strain differences in the collective behaviour of zebrafish (danio rerio) in heterogeneous environment», *Royal Society Open Science*, vol. 3, n° 10, p. 160451. [145](#), [153](#)
- Spence, R., M. Fatema, M. Reichard, K. Huq, M. Wahab, Z. Ahmed et C. Smith. 2006, «The distribution and habitat preferences of the zebrafish in bangladesh», *Journal of Fish Biology*, vol. 69, n° 5, p. 1435–1448. [145](#)
- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, danio rerio», *Biological Reviews*, vol. 83, n° 1, p. 13–34. [145](#)
- Strandburg-Peshkin, A., C. R. Twomey, N. W. Bode, A. B. Kao, Y. Katz, C. C. Ioannou, S. B. Rosenthal, C. J. Torney, H. S. Wu, S. A. Levin et collab.. 2013, «Visual sensory networks and effective information transfer in animal groups», *Current Biology*, vol. 23, n° 17, p. R709–R711. [147](#)
- Sueur, C., J.-L. Deneubourg et O. Petit. 2011a, «From the first intention movement to the last joiner : macaques combine mimetic rules to optimize their collective decisions», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 278, n° 1712, p. 1697–1704. [144](#)

- Sueur, C., A. J. King, L. Conradt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C. M. Schaffner, L. Williams, D. Zinner et F. Aureli. 2011b, «Collective decision-making and fission–fusion dynamics : a conceptual framework», *Oikos*, vol. 120, n° 11, p. 1608–1617. [144](#)
- Suriyampola, P. S., D. S. Shelton, R. Shukla, T. Roy, A. Bhat et E. P. Martins. 2016, «Zebrafish social behavior in the wild», *Zebrafish*, vol. 13, n° 1, p. 1–8. [145](#)
- Wiens, J. A. 1976, «Population responses to patchy environments», *Annual review of ecology and systematics*, p. 81–120. [145](#)

Chapitre 9

The perpetual Y-maze : a journey in a fragmented environment

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In prep.

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9.1 Résumé

Nous analysons le comportement collectif de vingt groupes de 5 *Danio rerio* (zebrafish) de type AB dans une version actualisée du labyrinthe en Y. Notre labyrinthe s'inspire de nombreuses études portant sur les prises de décision collectives dans des labyrinthes en Y et de nos observations de multiples tailles de groupes de zebrafish effectuées dans un autre type d'environnement contraint (deux chambres reliées par un couloir). Tout au long des 20 réplicats les zebrafish nagent sans interruption et parcourent le labyrinthe en passant dans chaque salle. Nous identifions les positions de chaque individus, relevons différentes mesures au niveau du groupe et analysons les choix effectués par le groupe ainsi que le leadership. Ce nouveau type de labyrinthe présente nombre d'avantages : il est dorénavant possible, en un minimum de réplicats, de récupérer de grandes quantités de données sur les comportements collectifs, le leadership et la prise de décision. En effet, nous avons remarqué que les zebrafish présentent un taux d'habituation au labyrinthe négligeable durant les première 45 minutes d'exploration. En réitérant les mesures effectuées dans le précédent labyrinthe (deux chambres reliées par un couloir), nous mettons en évidence une stabilité dans les transitions collectives du zebrafish quelque soit son environnement. Enfin, nous remarquons que les zebrafish partagent généralement le leadership : dans seulement un quart des réplicats, un des poissons s'imposait dans plus de 50% des départs collectifs.

9.2 Abstract

We explore the collective behaviour of 20 groups of 5 AB zebrafish (*Danio rerio*) in a new type of Y-maze (perpetual Y-maze). The set-up is inspired by studies of collective decision making in typical Y-maze and the observations of the behaviour of several groups of zebrafish in other constrained set-ups. The zebrafish swim continuously and travel through the different areas. We track the positions and the identities of the fish and compute the measures at the group level and analyse decision making and leadership. First, the interest of the perpetual Y-maze relies in the advantage it offers. It is therefore possible to perform massive data gathering on decision making with few replicates since habituation occurs after 45 minutes of exploration. Second, we noticed that the collective behaviour of zebrafish is relatively stable across the environment if we compare the results obtained in another type of constrained set-up. Third, we show that the leadership of zebrafish is generally shared between the members of the shoal.

9.3 Introduction

Collective movements [Engeszer et collab. \[2007\]](#); [Hemelrijk et Hildenbrandt \[2012\]](#); [Herbert-Read et collab. \[2011\]](#); [Parrish et collab. \[2002\]](#); [Petit et Bon \[2010\]](#); [Radakov \[1973\]](#); [Sueur et collab. \[2011a,b\]](#), food collections [Detrain et Deneubourg \[2008\]](#) or nest site selections [Amé et collab. \[2006\]](#); [Dahlbom et collab. \[2011\]](#); [Franks et collab. \[2002\]](#); [Rieucou et collab. \[2010\]](#) are contexts linked with the collective decision making. During nest site selections, social individuals have to choose among several alternatives in a complex environment. It has already been shown that for social species, the selection of such sites involves a collective participation that ranges from few individuals, for example the personal leadership of mountain gorillas [Watts \[2000\]](#) or the distributed leadership of three-spined stickleback [Harcourt et collab. \[2009\]](#), to the whole group, for example the consensus for the honey bees [Oldroyd et collab. \[2008\]](#), the ants [Pratt et collab. \[2002\]](#) or the golden shiners [Couzin et collab. \[2011\]](#).

Many constrained environments or mazes, such as corridor type [Engeszer et collab. \[2007, 2004\]](#); [Pettersson et Brönmark \[1993\]](#), Y-maze [Ward et collab. \[2011\]](#), T-maze [Kistler et collab. \[2011\]](#) or Plus-maze [Miller et collab. \[2013\]](#); [Sison et Gerlai \[2010\]](#), have been built to test the individual or the collective behaviours of numerous species. These constrained set-ups engage the animals to transit alone or in group through the corridors, from sites to sites, which is nothing more than decision makings. The main interest of these set-ups is their versatilities, they are used for other ethological issues such as pre-departure behaviours [Bourjade et collab. \[2015, 2009\]](#), leadership [Bourjade et collab. \[2015\]](#); [Ward et collab. \[2013\]](#) or initiation behaviours [Bourjade et collab. \[2009\]](#); [Rosenthal et collab. \[2015\]](#); [Ward et collab. \[2013\]](#), follower organisations [Ward et collab. \[2013\]](#), progression of individuals or groups and sites transitions [Harcourt et collab. \[2009\]](#); [Nakayama et collab. \[2012a, 2011\]](#).

However, Y-maze, T-maze or Plus-maze are used generally to observe unique decision making events : during the trials, the animals are released in the set-up, move through the corridor then make a decision by choosing a site. After this last task, experimentators put them back either in their breeding tank [Miller et collab. \[2013\]](#); [Ward et collab. \[2013, 2011\]](#) for few days or in front of the decision zone after few hours (center of the Y, T or +) [Miller et collab. \[2013\]](#); [Pearce \[2013\]](#), depending on the research. For exemple, [Ward et al. Ward et collab. \[2011\]](#) have shown that mosquitofish, *Gambusia holbrooki*, choose the arm without the predator or test the preference of damselfish *Dascyllus aruanus* for a piece of coral or a strip of coral sand and pebbles [Ward et collab. \[2013\]](#). [Miller et al. Miller et collab. \[2013\]](#) have shown that mixed societies of golden shiners, *Notemigonus crysoleucas*, trained by associative learning to choose one out of two different alternatives (arms) respectively, will choose preferentially a third arm that results from a mix of the two others.

Moreover, most of these experiments with mazes come under the choice between qualitatively different alternatives and provide numerous insights of individual and collective preferences. However, asymmetric choices may hide the collective decisions that result from internal processes of decision-making of the group. This is why we propose a new version of the Y-maze that could be adapted for the other kinds of mazes very simply. Unlike the typical Y-maze, in the perpetual Y-maze version no starting nor ending zones has to be defined. Each of the three arms of the Y-maze are identical and composed of a corridor and a chamber (Figure 9.1). The interest of such set-up is that once the animals made a choice, engaged in the corridor and reached a room, no human intervention is needed : the present room becomes the starting room and the animals continue to explore their environment. Hence, zebrafish make successive choices, between several alternatives, during one hour replicates. In the decision zone, they have the choice between the two rooms in front of them and the room where they came from. As an exemple, we obtain in mean 202 decision events with a small rate of habituation for the twenty replicates of one hour.

Here we investigate the influence of the leader on zebrafish collective decision making. In particular, we would like to characterise the dynamics of the choices for a group size of 5 AB zebrafish in a constrained environment. Y-maze seems to be the set-up that will help us to answer to our question. Zebrafish are gregarious vertebrate model organisms used in behavioural [Norton et Bally-Cuif \[2010\]](#); [Oliveira \[2014\]](#) and learning studies [Al-Imari et Gerlai \[2008\]](#); [Colwill et collab. \[2005\]](#). They behave in groups in the nature as much as in the laboratory [Engeszer et collab. \[2007\]](#); [McClure et collab. \[2006\]](#); [Spence et collab. \[2008\]](#). These fish come from India and live in groups of variable sizes [Parichy \[2015\]](#); [Pritchard et collab. \[2001\]](#); [Suriyampola et collab. \[2016\]](#) depending on the region, the quality of the water (pH, temperature) and the presence of predators, in a wide variability of habitats with varying structural complexities [Arunachalam et collab. \[2013\]](#); [Suriyampola et collab. \[2016\]](#). We based our experimental method on the observations of fish swimming in a Y-maze composed of 3 identical rooms connected by 3 identical corridors joining in the center of the *Y*. This set-up is a new variation of the previous one we built in [Collignon et collab. \[2017\]](#); [Séguret et collab. \[2017\]](#), *2 rooms connected by a corridor*, and is always evoking irrigation canals [Spence et collab. \[2006\]](#) and patchy environments [Wiens \[1976\]](#).

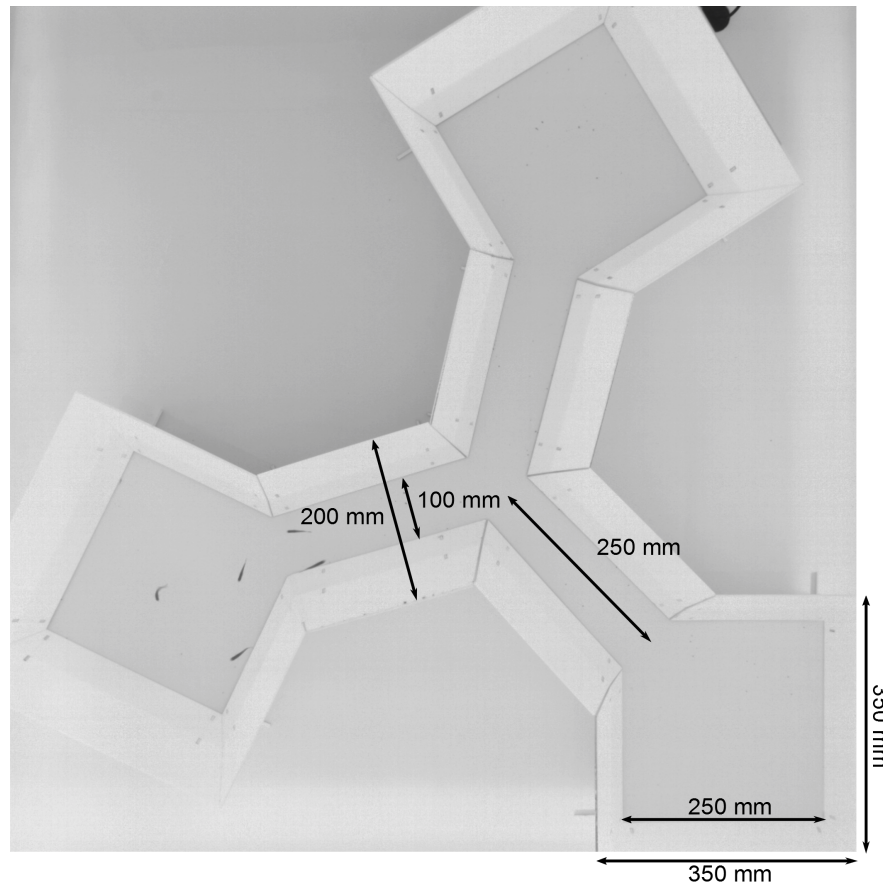


FIGURE 9.1 – **Experimental area** composed by three square rooms (300 mm x 300 mm) connected by corridors (200 mm x 10 mm). We observed 12 groups of 5 zebrafish swimming during one hour to study the collective behaviours of the fish in a fragmented environment.

9.4 Results

9.4.1 Habituation

We present here the results of collective decisions computed for 20 replicates of groups of 5 AB zebrafish swimming in the Y-maze (Figure 9.1), without human interruption during one hour. We tested each zebrafish only once to avoid potential learning and to test only naive individuals. We compute for four time intervals of 15 minutes the number of transitions between the two rooms (Figure 9.2). The first interval is based on 1161 values, the second on 1052 values, the third on 976 values and the last one on 850 values. We see that the number of transitions decrease through the time. A Kruskal-Wallis test shows significant differences between the time travels for each interval ($p - value < 0.01$). A Tukey's honest significant difference criterion shows that $p - value < 0.01$ between the intervals $[0, 15]$ and $[45, 60]$; for the intervals $[0, 15]$, $[15, 30]$ and $[30, 45]$, $p - value > 0.01$ or $[15, 30]$, $[30, 45]$ and $[45, 60]$, $p - value > 0.01$.

We compute for four time intervals of 15 minutes the travel time between the rooms (Figure 9.3). The first interval is based on 867 values, the second on 783 values, the third

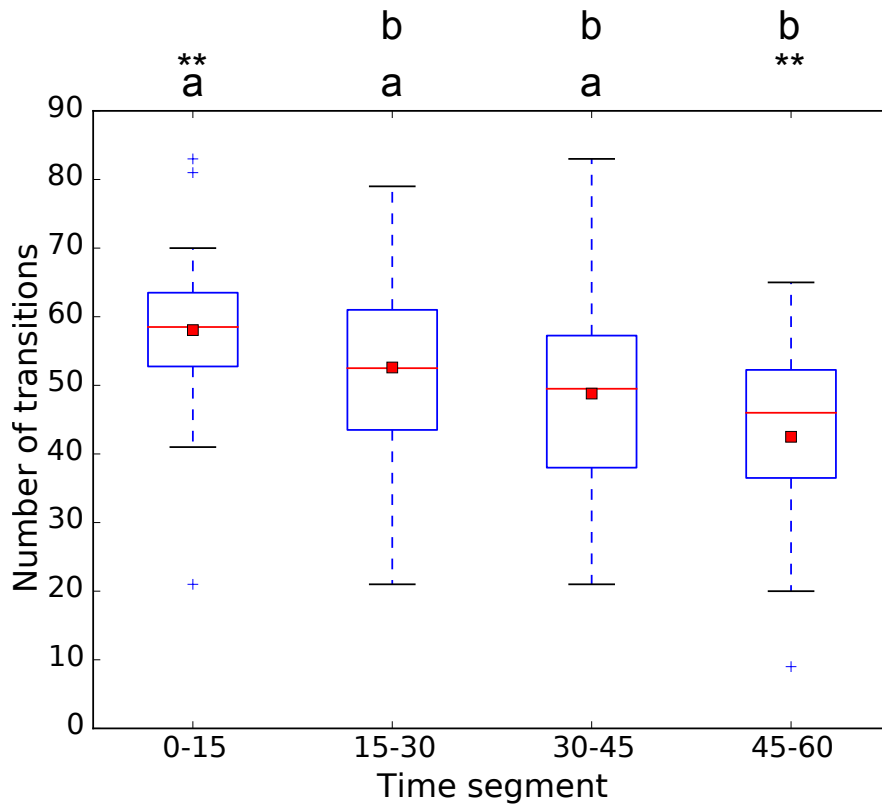


FIGURE 9.2 – **Number of transitions between two rooms** at different steps of the experiment for 20 replicates with 5 zebrafish. The red line shows the median and the red square is the mean. * = p -value < 0.05, ** = p -value < 0.01, *** = p -value < 0.001, ns = non significant.

on 722 values and the last one on 636 values. A Kruskal-Wallis test shows that there is no significant differences between the time travels for each interval (p -value > 0.05). Whatever the time interval (i.e. during the beginning or the end of the replicates), zebrafish cross the corridors in almost 4 seconds.

9.4.2 Collective decisions

Then we focus on the transitions in groups of 4 or more zebrafish (Figure 9.4). We reveal that most of the time groups of zebrafish make decisions for alternatives located in front of them (left or right) : the mean of the probability for zebrafish to go to the left is 41.3%, to the right is 42.7% and to make a U-turn is 16.0%. The transitions to the left and to the right rooms by the group are significantly higher than U-turns (Kruskal-Wallis, p -value < 0.001, Tukey's honest significant difference criterion, p -value < 0.001 for U-turns versus Left and p -value < 0.001 for U-turns versus Right). For the left, the right and the u-turns there are 20 values each.

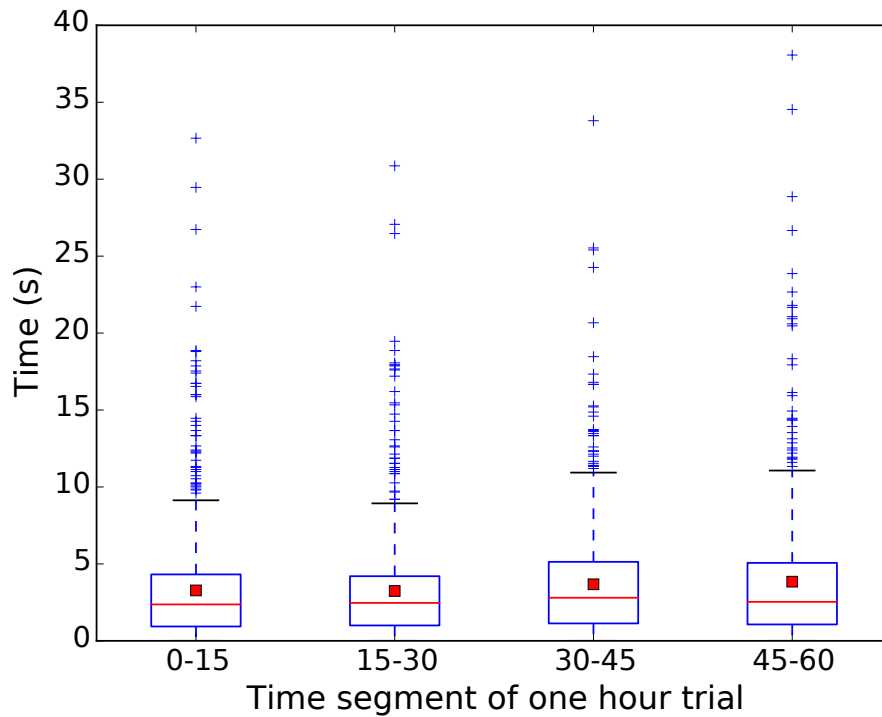


FIGURE 9.3 – **Travel time between two rooms** at different steps of the experiment for 20 replicates with 5 zebrafish. The red line shows the median and the red square is the mean. A Kruskal-Wallis test shows no significant evolution during one hour of experiment ($p > 0.05$).

9.4.3 Leadership

In this section, we characterize the leadership. Because of the idTracker software, we are able to identify and to follow each fish. We consider a leader as the first zebrafish that leaves a room (initiation) and is followed by all the group (collective departure). In the Figure 9.5, we reveal that there is no change of leadership between the exit of a room (leader) and the exit of the triangle of decision – junction of the corridors – (decision maker) whatever the fish. Also, this figure shows that the leader / decision maker is in front of the group.

In the Figure 9.6, we reveal for the 20 replicates (A to T) the proportion of collective departures initiated by each fish and rank the groups according to the score of their member that led the highest proportion of departure. There is no replicate where the distributions of the initiations are equally shared by the zebrafish. In 25% of the replicates (P to T), we show that one fish takes the position of the leader for at least 50% of the initiations. We call these individuals the *super leaders*.

In the Figure 9.7, for all replicates we look at the changes of leadership through the time according to 4 time intervals. We define the change of leadership as a change of initiator between two simultaneous initiations. There are 957 values for the interval 0 to 15 minutes, 827 values for the interval 15 to 30 minutes, 721 values for the interval 30 to 45 minutes and 641 values for the interval 45 to 60 minutes. The mean of the proportions of

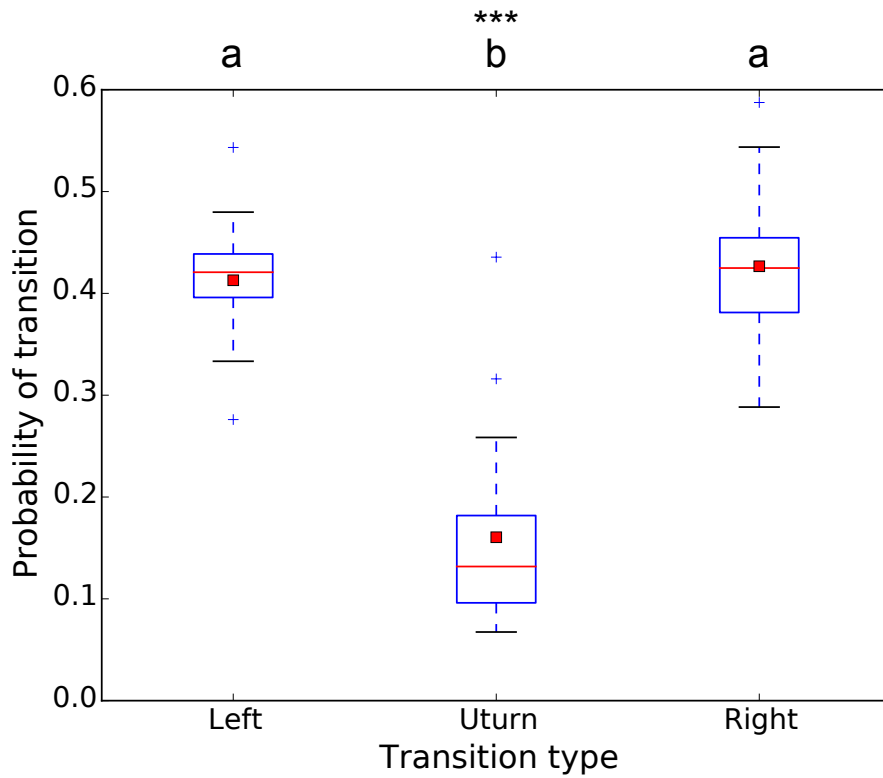


FIGURE 9.4 – **Transition probability for each fish** to choose Left, Right or U-turn during a transition event of the majority of the group (≥ 4 individuals). The red line shows the median and the red square is the mean. Zebrafish have the same probabilities to turn Left or right similar and a lower probability to perform a U-turn. * = p -value < 0.05, ** = p -value < 0.01, *** = p -value < 0.001, ns = non significant.

changes in leadership oscillate around 70% whatever the time interval. A Kruskal-Wallis test shows that whatever the time interval, there is no significant differences between the distributions of the changes in the leadership (p -value > 0.05).

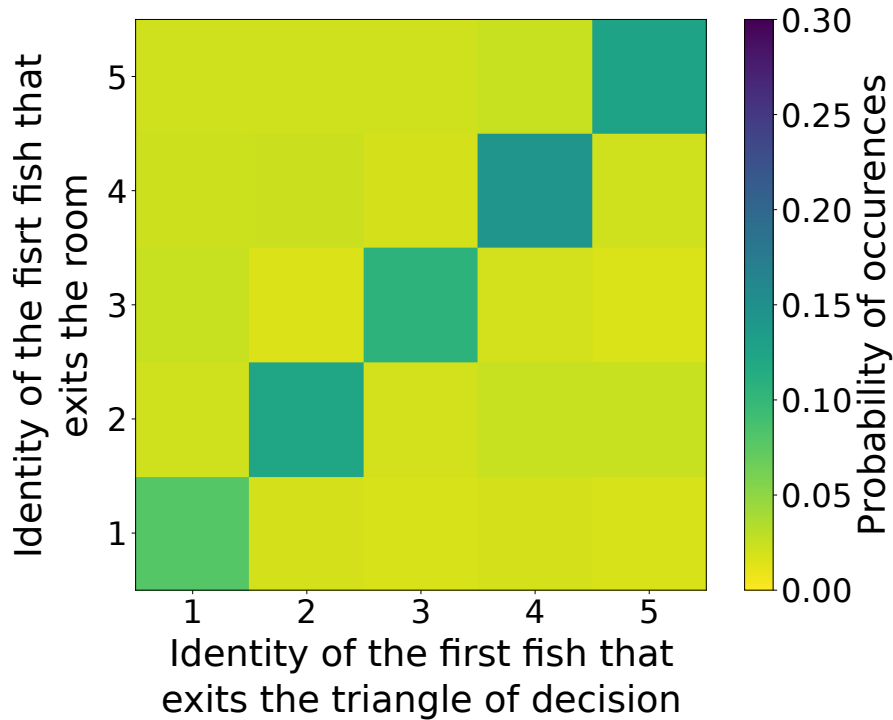


FIGURE 9.5 – **Change of leadership between the exit of a room and the exit of the triangle of decision.** Generally, the first fish that exits the room is the first that exits the triangle of decision, namely the first fish making a decision.

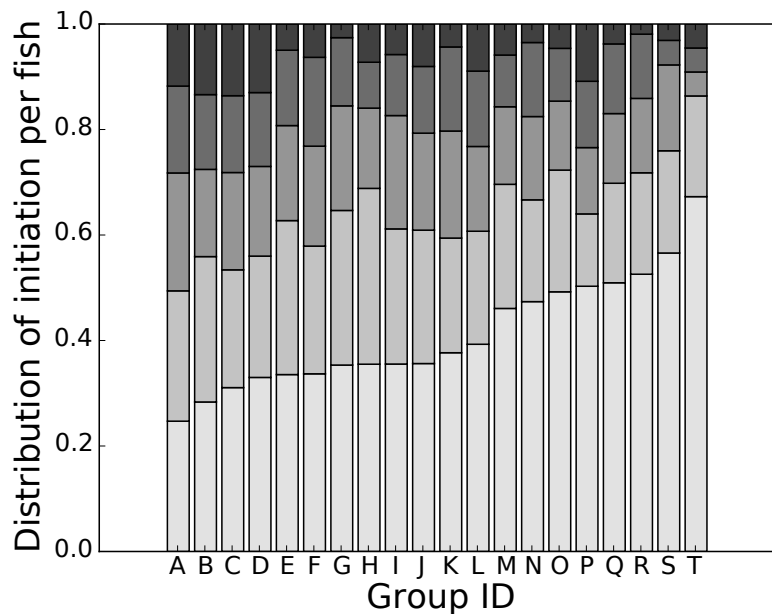


FIGURE 9.6 – **Proportion of collective departures** led by each group member. The fish are ranked in each group according to the proportion of initiation that they made and the groups are ranked according to the highest proportion of departure shown by a group member. The leadership is unequally shared between individuals. In 5 groups, one individual leads the group for at least 50% of the initiations.

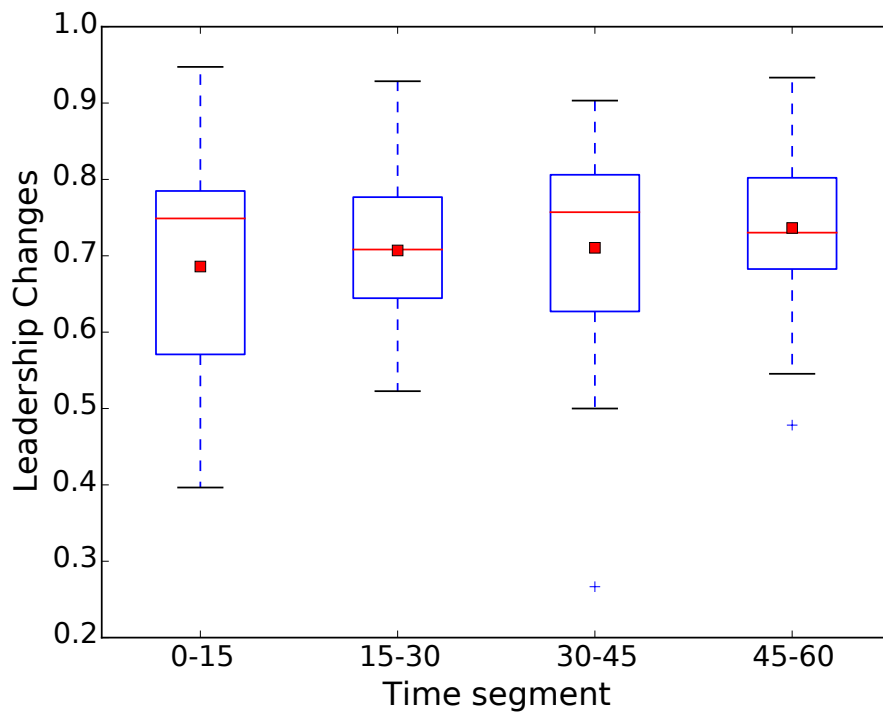


FIGURE 9.7 – **Leadership changes** at each transition with a high probability and during the whole duration of each replicate. The red line shows the median and the red square is the mean.

9.5 Discussion

We studied the leadership and the decision making of 20 different groups of 5 AB zebrafish in a Y-maze. Unlike typical Y-maze experiments [Burns et collab. \[2012\]](#); [Ward et collab. \[2011\]](#), our set-up is entirely homogeneous, with identical corridors or rooms. There is no ending room and we only interrupt each replicate after one hour, so that we can see whether or not leadership and the decision making evolve across the time. Before anything else, the [Figure 9.4](#) does not show particular bias of preference of the zebrafish to go to the left or to the right. We admit the set-up is unbiased : lighting is homogeneous, rooms are identical. In a previous article, we analysed the collective departures and oscillations of several group sizes of AB zebrafish in a patchy environment consisting in two rooms connected by a corridor [Collignon et collab. \[2017\]](#); [Séguret et collab. \[2017\]](#). We found that groups of 5 zebrafish made six times less U-turns than transitions (from a room to the other one) in groups of more than 4 individuals. In the Y-maze, we show that groups of 5 zebrafish make five times less U-turns than transitions (to the left and to the right) in groups of more than 4 ([Figure 9.4](#)). The group behave similarly when changing the environment. We did not find in the literature studies of groups of animals moving in different environments. It would be interesting to study the robustness of the collective behaviour among several environments and its evolutive advantage.

We already know that the personal motivation of the animals can produce an initiation of departure. This has been found for many species : *Equus burchellii* [Fischhoff et collab. \[2007\]](#), *Dicentrarchus labrax* [Millot et collab. \[2009\]](#) or *Gasterosteus aculeatus* [Nakayama et collab. \[2012b\]](#). We revealed here a wide variability of types of leaderships among the 20 tested groups ([Figure 9.6](#)). In most of the cases, the leadership switches without equal distribution between all the members of the groups and for some groups the leadership is partially unshared, as 50% of the initiations are performed by the same fish. We already know that personalities exist in the zebrafish and are related to the intrinsic propensity of each fish to explore new environments [Dahlbom et collab. \[2011\]](#); [Guayasamin \[2013\]](#). Moreover [Kurvers et collab. \[2009\]](#); [Leblond et Reeb \[2006\]](#); [Wilson et Godin \[2010\]](#) have shown that bolder individuals are predisposed towards leadership. Hence, for the groups of fish where one individual leads the initiations more than 50% of the time, we could wonder if they were composed of 4 shy individuals and 1 bold individual, or if it could exist different degrees of personality. In this case, it is possible that the boldness of the leaders is stronger than the boldness of other fish.

Although the wide range of leadership types (from shared to partially shared) and the decision of the whole group to perform a collective departure, the fish in front of the group is the unique decision maker ([Figure 9.5](#)). Often, the location of the future leader, in relation to the group, is of high importance. While for monkeys (*Cebus capucinus* or *Macaca*

mulatta), the individuals in the center of the group initiate collective departures [Leca et collab. \[2003\]](#); [Sueur et Petit \[2008\]](#), for fish (*Notemigonus crysoleucas*, *Rutilus rutilus* or *Gasterosteus aculeatus*), this role is attributed to the animals on the periphery of the group [Bumann et Krause \[1993\]](#); [Krause et collab. \[2000\]](#); [Reebs \[2000\]](#); [Rosenthal et collab. \[2015\]](#).

[Burns et al. Burns et collab. \[2012\]](#) tested 18 groups of 5 *Gambusia holbrooki* in a Y-maze and did 5 replicates for each group, at a rate of one replicate a day for each group. Once the fish made their decision they were captured and put back in their breeding tank. Unlike *Gambusia holbrooki* in a Y-maze where the "leadership switched between group members more often in an unfamiliar environment than when group members had experience of that same environment", the leadership of zebrafish does not evolve across the time (Figure 9.7). In the literature, their experiments were the closest from ours. Both of us, we tested the effect of unfamiliar (the first quarter of the hour of test) and familiar (the three last quarters of the hour of test) environments on leadership. We suggest that this contradiction between the leaderships in groups of zebrafish and mosquitofish may be due to their propensities to comprehend their territory and to deal with the group. It seems that zebrafish and mosquitofish have developed opposite adaptive collective behaviours. Mosquitofish are known to form highly hierarchical societies [Caldwell et Caldwell \[1962\]](#); [Chen et collab. \[2011\]](#) and our observations suggest that zebrafish share equally to partially informations and decision making (Figures 9.6 and 9.7). This hypothesis is strengthened by the Figures S 9.15 and S 9.16 : there is no clear leader and each fish from all kinds of personalities can initiate a collective departure. We already developed the hypothesis in [Collignon et collab. \[2017\]](#).

Also, we express reservations about the way experiments in mazes, generally based on repetitive tasks interrupted by humans, are performed and the signification of their results (Table 9.1). Actually, the animals may have understand a part of the purpose of the experiments in the mazes because each time the groups made a choice, they were put back in their breeding tank. It is therefore possible that individuals which initially lead the groups during the first replicate may reproduce this behaviour and reinforce it. We then may wonder if the fish are as naive as for the first replicate. This issue may be answered by few measures that are absent from the papers but easily and quickly computed : the travel time between the release of the animals and the instant after the decision making and the number of transitions across the time of the replicate. If the travel time or the number of transtions evolve across the replicate, it means that the animals may become familiar with the set-up or may understand its purpose. In this context the results could be biased. Figures 9.2 and 9.3 show that the number of transitions decreases slowly in time and the travel time through the corridors is relatively stable across the four time intervals. Also, in the Figure 9.4, we have already noticed that during binomial decision making events

the groups of zebrafish have no preference for one room over the other one. Hence, we have shown that zebrafish after one hour may be as unfamiliar with the set-up as at the beginning of the replicate or may not understand the purpose of the set-up (to make a decision between at least two alternatives).

Authors	Type of maze	Number of trials	Length of trials	Number of use of animals
Ward et al. Ward et collab. [2008]	Y-maze	320	few min	not known or 20 times
Sumpter et al. Sumpter et collab. [2008]	Y-maze	2200	few min	not known or 20 times
Couzin et al. Couzin et collab. [2011]	Y-maze like	108	not known	3 times
Ward et al. Ward et collab. [2011]	Y-maze	107 * 12 ** 13 ***	few sec few sec few sec	not known not known not known
Burns et al. Burns et collab. [2012]	Y-maze	90	not known	5 times
Ward et al. Ward et collab. [2012]	Y-maze	240	few min	only once
Benhaim et al. Benhaïm et collab. [2013]	T-maze like	90	10 min	3 times
Miller et al. Miller et collab. [2013]	Y-maze like	640	5 min	40 times
Kleiman et al. Kleiman et collab. [2014]	Plus-maze	44	5 min	only once

TABLEAU 9.1 – **Recent papers about the use of mazes for decision making studies** with fish and terrestrial vertebrates. min for minutes, sec for seconds, * replicates with 1 fish, ** replicates with 2 and 4 fish, *** replicates with 8 and 16 fish.

This is why we built the perpetual Y-maze. Its goal is to avoid interactions between the experimentator and the animals in order not to manipulate the naive behaviour of the animals. Moreover, Table 9.1, that sums up recent studies using mazes, shows that it can take a while to perform all the replicates to get enough data. We observe generally that the animals are used several times for the same experiments. Hence, in the perpetual Y-maze, we let the fish swimming freely and make choices several times. After one hour, the groups made in mean 202 decisions. Each day 5 replicates are processed, meaning

that in less than one week we tested 20 groups, namely more than 4000 decision events. Finally, the measures of the number of transitions and the travel time across the corridors could be considered together as elements related to the habituation. Our results suggest strongly that habituation across the time in the perpetual Y-maze is limited (Figures 9.2 , 9.3 and S 9.11).

9.6 Methods

9.6.1 Ethic statement

Fish experiments were performed in accordance with the recommendations and guidelines of the Buffon Ethical Committee (registered to the French National Ethical Committee for Animal Experiments #40) after submission to the state ethical board for animal experiments.

9.6.2 Animals and housing

We bred 600 AB strain laboratory wild-type zebrafish (*Danio rerio*) up to the adult stage and raised them under the same conditions in tanks of 3.5L by groups of 20 fish in a zebrafish aquatic housing system (ZebTEC rack from Tecniplast) that controls water quality and renew 10% of water in the system every hour. Zebrafish descended from AB zebrafish from different research institutes in Paris (Institut Curie and Institut du Cerveau et de la Moelle Épineuse). AB zebrafish show zebra skin patterns and have short tail and fins. They measure about 3.5 cm long. All zebrafish observed in this study were one year old at the time of the experiments. We kept fish under laboratory conditions : 27°C, 500µS salinity with a 10 :14 day :night light cycle, pH is maintained at 7.5 and nitrites (NO_2^-) are below 0.3 mg/L. Zebrafish are fed two times a day (Special Diets Services SDS-400 Scientific Fish Food).

9.6.3 Experimental setup

The experimental tank consists in a 1.2 m x 1.2 m tank confined in a 2 m x 2 m x 2.35 m experimental area surrounded by white sheets, in order to isolate the experiments and homogenise luminosity. The three squared rooms (300 mm x 300 mm) connected by corridors (200 mm x 10 mm) starting at one corner of each room (Fig. 9.1) have been designed on a Computer-Aided Design (CAD) software and cut out from Poly(methyl methacrylate) (PMMA) plates of 0.003 m thickness. Each wall are tilted, (20° from the vertical) to the outside with a vertical height of 0.14 m, to avoid the presence of blind zones for the camera placed at the vertical of the tank. The water depth is at 6 cm in order to keep the fish in a

nearly two-dimensional space to facilitate their tracking, the pH is maintained at 7.5 and Nitrites (NO_2^-) are below 0.3 mg/L. A high resolution camera (2048 px x 2048 px, Basler Scout acA2040-25gm) is placed above the water surface (160 cm), at the vertical, and records the experiment at 15 fps (frame per second). The luminosity is ensured by 4 LED lamps of 33W (LED LP-500U, colour temperature : 5500 K - 6000 K) placed on each corner of the tank, above the aquarium and directed towards the walls to provide indirect lightning.

9.6.4 Experimental procedure

We recorded the behaviour of zebrafish swimming in the set-up, during one hour, and did 12 replicates of groups of 5 zebrafish. Before each replicate, the starting room, from which the fish are released, is chosen randomly. Then, the fish were placed with a hand net in a cylindrical arena (20 cm diameter) made of plexiglas in the center of the selected room. Following a 5 minutes acclimatization period, the camera started recording, the fish were released and free to swim in the set-up. After one hour, the record stops and the fish are caught by a hand net and replaced in the rearing facilities. The fish were randomly selected regardless of their sex and each fish was never tested twice to prevent any form of learning.

9.6.5 Tracking & data analysis

Today, the studies on animal collective behaviours use methodologies based on massive data gathering, for exemple for flies (*Drosophila melanogaster*) Branson et collab. [2009]; Dankert et collab. [2009], birds (*Sturnus vulgaris*) Ballerini et collab. [2008]; Miller et Gerlai [2007, 2011], fish (*Notemigonus crysoleucas*) Strandburg-Peshkin et collab. [2013]. Our experiments were tracked by post-processing ("off-line") with the idTracker software to identify each fish and their positions Pérez-Escudero et collab. [2014]. This multitracking software extract specific characteristics of each individual and uses them to identify the animal throughout the video. This method avoids error propagation and is able to successfully solve crossing, superposition and occlusion problems. Each replicate consists of 270000 positions : $P(x, y, t)$ with coordinates, x and y , and the time, t .

We build the trajectories of each fish and compute individuals and collective measures (position in the arena, speed, acceleration). The instantaneous speed v_t was calculated on three positions and thus computed as the distance between $P(x, y, t - 1)$ and $P(x, y, t + 1)$ divided by 2 time steps while the instantaneous acceleration was computed as $\Delta s / \Delta t$.

9.7 Supplementary information and figures

Supplementary figures of "The collective behaviour of zebrafish (*Danio rerio*) in a fragmented environment".

9.7.1 Habituation

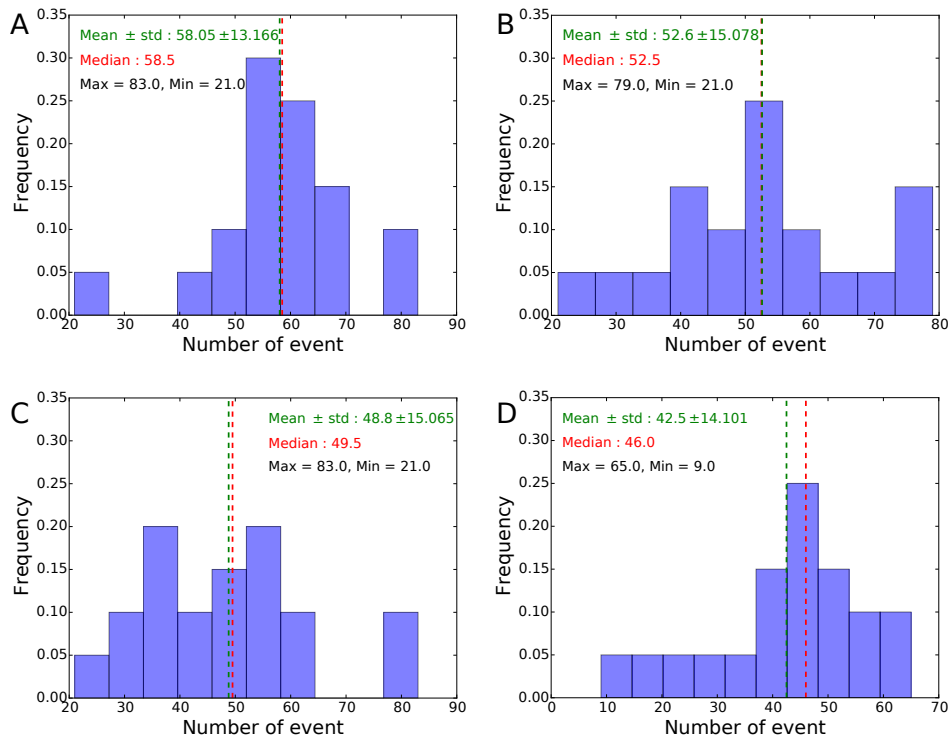


FIGURE 9.8 – **Distributions of the number of transitions between the rooms.** (A) For the interval 0 to 15 minutes, (B) for the interval 15 to 30 minutes, (C) for the interval 30 to 45 minutes, (D) for the interval 45 to 60 minutes. The red dashed lines show the medians and the green the means.

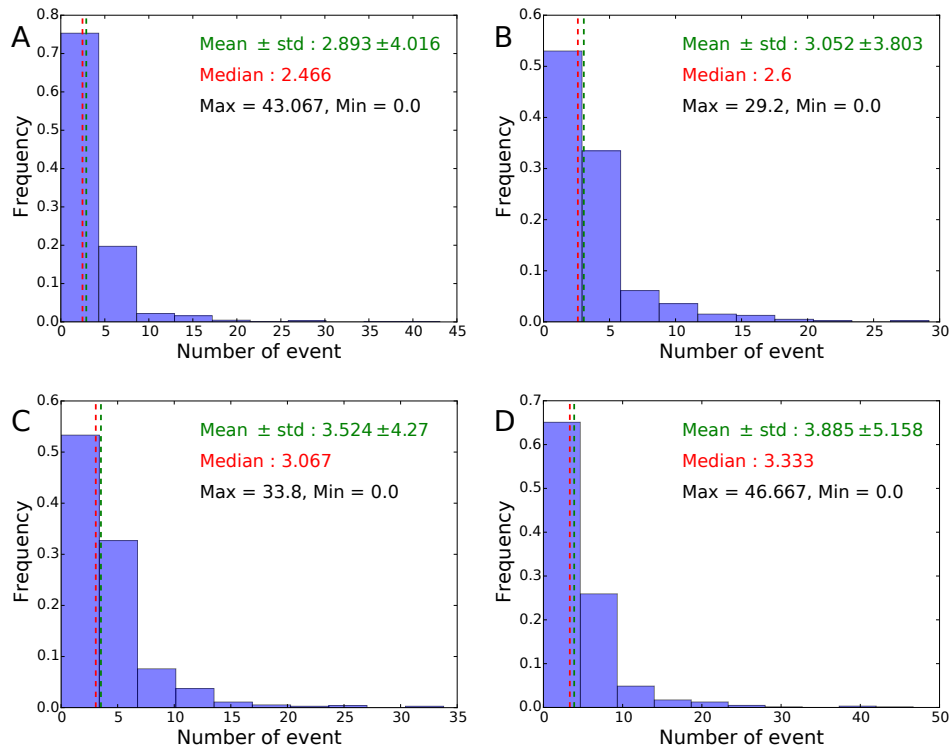


FIGURE 9.9 – **Distributions of the time travel between the rooms.** (A) for the interval 0 to 15 minutes, (B) for the interval 15 to 30 minutes, (C) for the interval 30 to 45 minutes, (D) for the interval 45 to 60 minutes. The red dashed lines show the medians and the green the means.

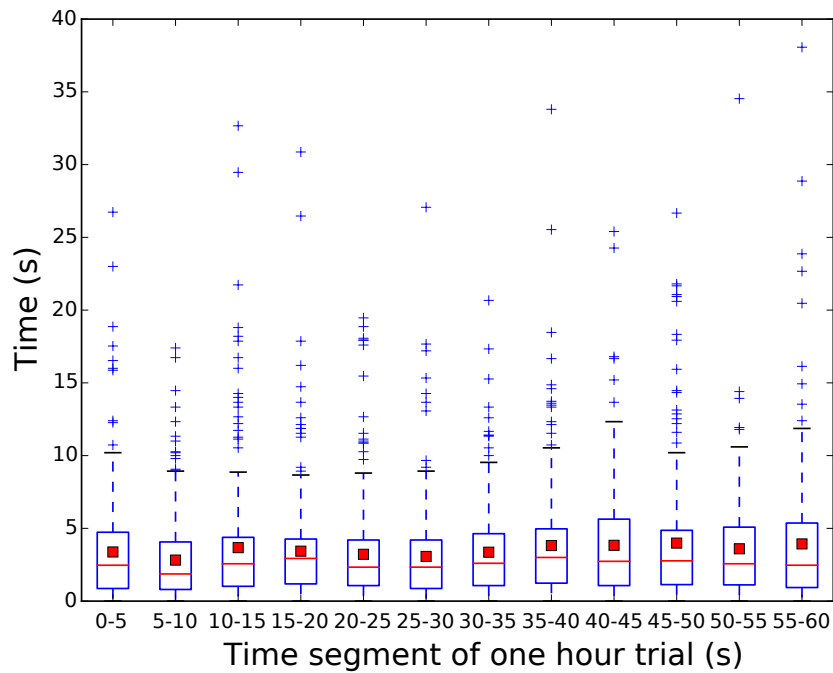


FIGURE 9.10 – **Travel time between two rooms** at different steps of the experiment for 20 replicates with 5 zebrafish. The red line shows the median and the red square is the mean. A Kruskal-Wallis test shows no significant evolution during one hour of experiment ($p > 0.05$).

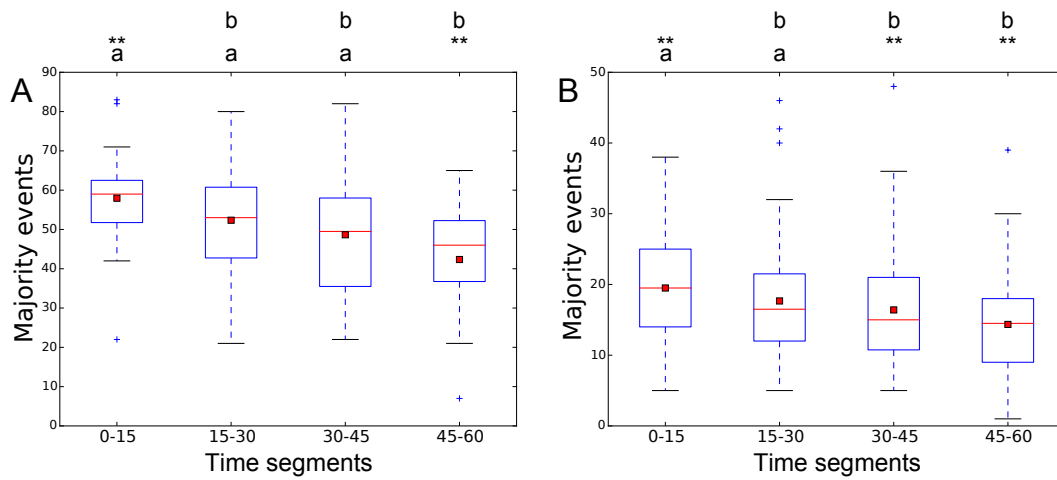


FIGURE 9.11 – **Number of majority events** at different steps of the experiment for 20 replicates with 5 zebrafish. (A) in the corridors, (B) in the rooms. The red line shows the median and the red square is the mean. (A) The number of majority events in the corridor are significantly higher for the time interval [0, 15] than [45, 60] (Kruskal-Wallis, p -value < 0.01, Tukey's honest significant difference criterion, p -value < 0.01 for [0, 15] versus [45, 60]). (B) The number of majority events in the corridor are significantly higher for the time interval [0, 15] than [45, 60] (Kruskal-Wallis, p -value < 0.01, Tukey's honest significant difference criterion, p -value < 0.01 for [0, 15] versus [30, 45] and for [0, 15] versus [45, 60]). * = p -value < 0.05, ** = p -value < 0.01, *** = p -value < 0.001, ns = non significant.

9.7.2 Collective decisions

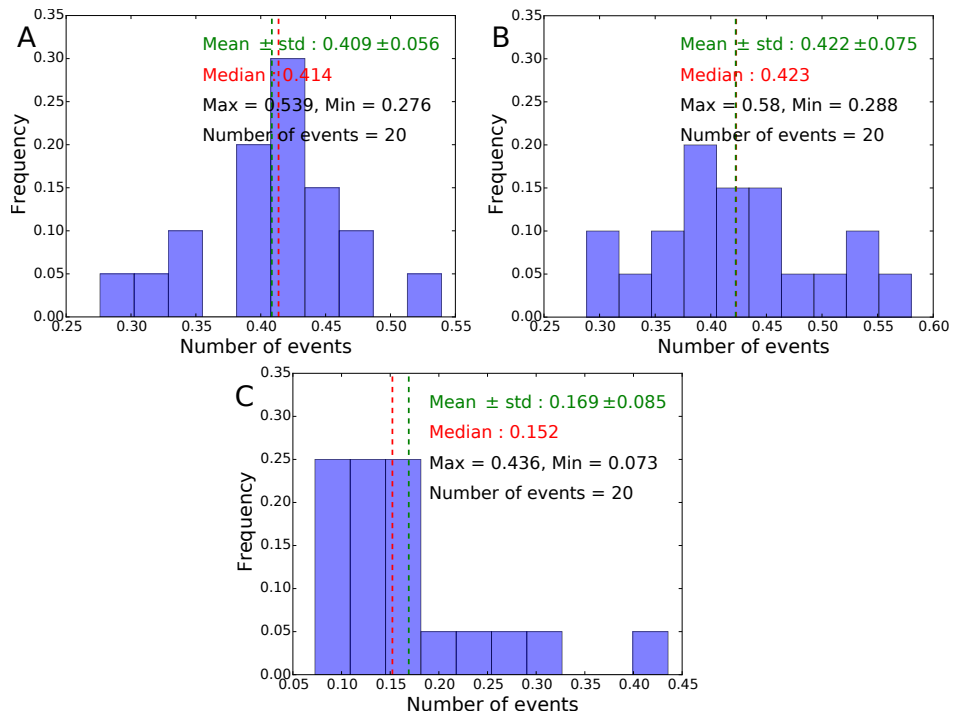


FIGURE 9.12 – Distributions of the decisions (A) to the left, (B) to the right and (C) as a urn.

9.7.3 Leadership

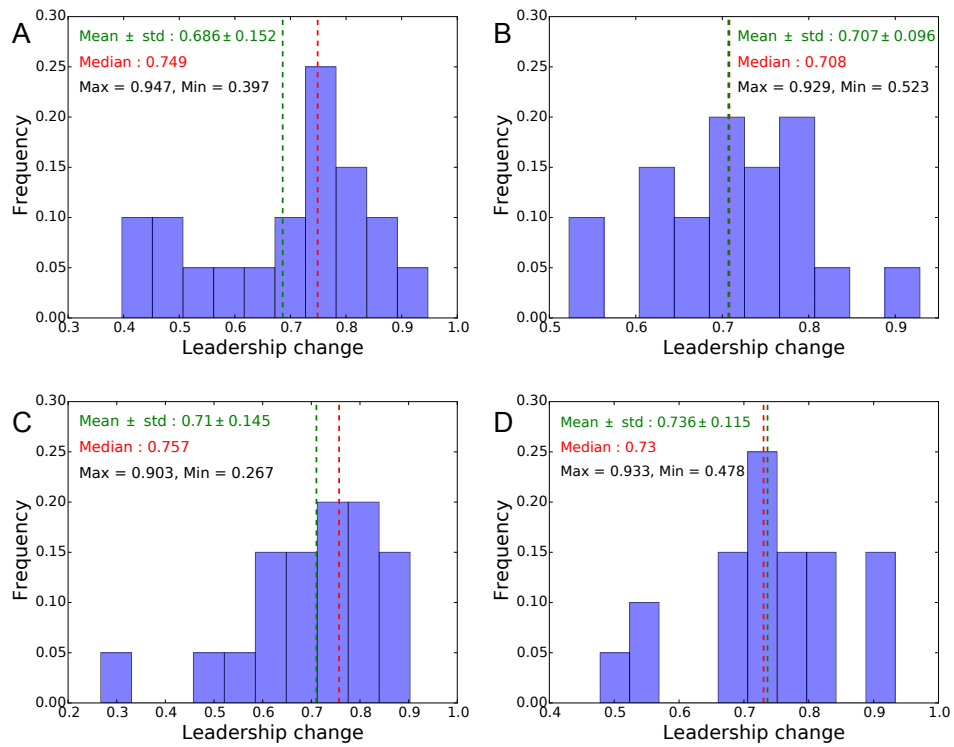


FIGURE 9.13 – **Distributions of the changes of leadership.** (A) For the interval 0 to 15 minutes, (B) for the interval 15 to 30 minutes, (C) for the interval 30 to 45 minutes, (D) for the interval 45 to 60 minutes.

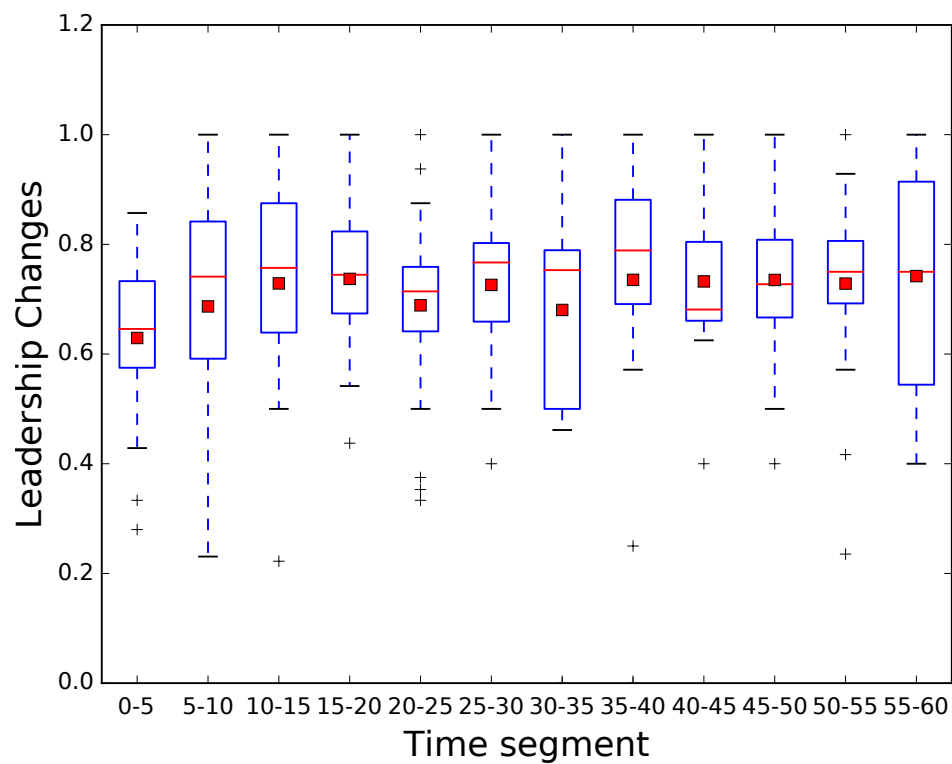


FIGURE 9.14 – **Leadership changes** at each transition with a high probability and this during the whole replicates. The red line shows the median and the red square is the mean.

The Figure S 9.15 shows that the number of successful collective departures is proportional to the number of attempts. We consider as a successful collective departure an event when all the group moves from a room to another one. The attempts are all the events where at least a fish leaves a room followed or not by its conspecifics.

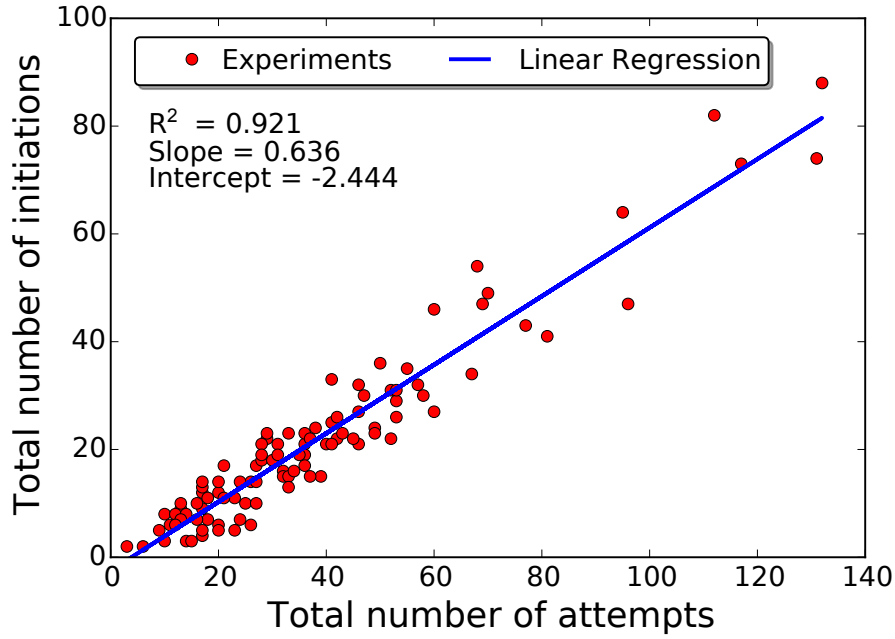


FIGURE 9.15 – **Successful collective departures and collective departure attempts of the initiator.** The number of successful collective departures is proportional to the number of attempts.

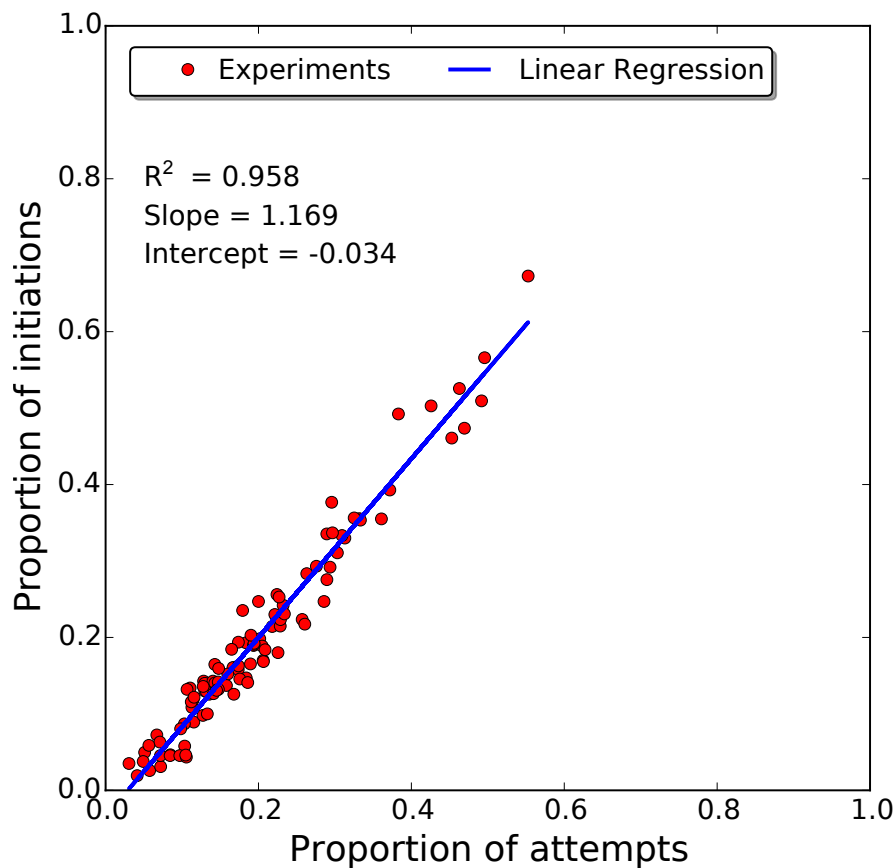


FIGURE 9.16 – Successful collective departures and collective departure attempts of the initiator. Proportion of initiations related to the proportion of attempts.

9.8 Références

- Al-Imari, L. et R. Gerlai. 2008, «Sight of conspecifics as reward in associative learning in zebrafish (*danio rerio*)», *Behavioural brain research*, vol. 189, n° 1, p. 216–219. [174](#)
- Amé, J.-M., J. Halloy, C. Rivault, C. Detrain et J. L. Deneubourg. 2006, «Collegial decision making based on social amplification leads to optimal group formation», *Proceedings of the National Academy of Sciences*, vol. 103, n° 15, p. 5835–5840. [173](#)
- Arunachalam, M., M. Raja, C. Vijayakumar, P. Malaiammal et R. L. Mayden. 2013, «Natural history of zebrafish (*danio rerio*) in india», *Zebrafish*, vol. 10, n° 1, p. 1–14. [174](#)
- Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini et collab.. 2008, «Interaction ruling animal collective behavior depends on topological rather than metric distance : Evidence from a field study», *Proceedings of the national academy of sciences*, vol. 105, n° 4, p. 1232–1237. [185](#)
- Benhaïm, D., M.-L. Bégout, G. Lucas et B. Chatain. 2013, «First insight into exploration and cognition in wild caught and domesticated sea bass (*dicentrarchus labrax*) in a maze», *PloS one*, vol. 8, n° 6, p. e65872. [183](#)

- Bourjade, M., B. Thierry, M. Hausberger et O. Petit. 2015, «Is leadership a reliable concept in animals? an empirical study in the horse», *PLoS one*, vol. 10, n° 5, p. e0126344. [173](#)
- Bourjade, M., B. Thierry, M. Maumy et O. Petit. 2009, «Decision-making in przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements», *Ethology*, vol. 115, n° 4, p. 321–330. [173](#)
- Branson, K., A. A. Robie, J. Bender, P. Perona et M. H. Dickinson. 2009, «High-throughput ethomics in large groups of *Drosophila*», *Nature methods*, vol. 6, n° 6, p. 451–457. [185](#)
- Bumann, D. et J. Krause. 1993, «Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*)», *Behaviour*, vol. 125, n° 3, p. 189–198. [182](#)
- Burns, A. L., J. E. Herbert-Read, L. J. Morrell et A. J. Ward. 2012, «Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments», *PLoS One*, vol. 7, n° 5, p. e36567. [181](#), [182](#), [183](#)
- Caldwell, M. C. et D. K. Caldwell. 1962, «Monarchistic dominance in small groups of captive male mosquitofish, *Gambusia affinis patruelis*», *Bulletin of the Southern California Academy of Sciences*, vol. 61, n° 1, p. 37–44. [182](#)
- Chen, T., M. Beekman et A. J. Ward. 2011, «The role of female dominance hierarchies in the mating behaviour of mosquitofish», *Biology letters*, vol. 7, n° 3, p. 343–345. [182](#)
- Collignon, B., A. Séguret, L. Cazenille, Y. Chemtob et J. Halloy. 2017, «Collective departures in zebrafish : profiling the initiators», *arXiv preprint arXiv:1701.03611*. [174](#), [181](#), [182](#)
- Colwill, R. M., M. P. Raymond, L. Ferreira et H. Escudero. 2005, «Visual discrimination learning in zebrafish (*Danio rerio*)», *Behavioural Processes*, vol. 70, n° 1, p. 19–31. [174](#)
- Couzin, I. D., C. C. Ioannou, G. Demirel, T. Gross, C. J. Torney, A. Hartnett, L. Conradt, S. A. Levin et N. E. Leonard. 2011, «Uninformed individuals promote democratic consensus in animal groups», *science*, vol. 334, n° 6062, p. 1578–1580. [173](#), [183](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*Danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [173](#), [181](#)
- Dankert, H., L. Wang, E. D. Hoopfer, D. J. Anderson et P. Perona. 2009, «Automated monitoring and analysis of social behavior in *Drosophila*», *Nature methods*, vol. 6, n° 4, p. 297–303. [185](#)
- Detrain, C. et J.-L. Deneubourg. 2008, «Collective decision-making and foraging patterns in ants and honeybees», *Advances in insect physiology*, vol. 35, p. 123–173. [173](#)
- Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan et D. M. Parichy. 2007, «Timing and plasticity of shoaling behaviour in the zebrafish, *Danio rerio*», *Animal behaviour*, vol. 74, n° 5, p. 1269–1275. [173](#), [174](#)

- Engeszer, R. E., M. J. Ryan et D. M. Parichy. 2004, «Learned social preference in zebrafish», *Current Biology*, vol. 14, n° 10, p. 881–884. [173](#)
- Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, H. M. Larkin, M.-J. Sellier et D. I. Rubenstein. 2007, «Social relationships and reproductive state influence leadership roles in movements of plains zebra, *equus burchellii*», *Animal Behaviour*, vol. 73, n° 5, p. 825–831. [181](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [173](#)
- Guayasamin, O. 2013, «Personality matters : A quantitative comparison of asocial and social behaviors in the zebrafish (*danio rerio*)», . [181](#)
- Harcourt, J. L., T. Z. Ang, G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Social feedback and the emergence of leaders and followers», *Current Biology*, vol. 19, n° 3, p. 248–252. [173](#)
- Hemelrijk, C. K. et H. Hildenbrandt. 2012, «Schools of fish and flocks of birds : their shape and internal structure by self-organization», *Interface focus*, p. rfs20120 025. [173](#)
- Herbert-Read, J. E., A. Perna, R. P. Mann, T. M. Schaerf, D. J. Sumpter et A. J. Ward. 2011, «Inferring the rules of interaction of shoaling fish», *Proceedings of the National Academy of Sciences*, vol. 108, n° 46, p. 18 726–18 731. [173](#)
- Kistler, C., D. Heggin, H. Würbel et B. König. 2011, «Preference for structured environment in zebrafish (*danio rerio*) and checker barbs (*puntius oligolepis*)», *Applied Animal Behaviour Science*, vol. 135, n° 4, p. 318–327. [173](#)
- Kleiman, M., S. Bodek et D. Eilam. 2014, «Who are the bosses? group influence on the behavior of voles following owl attack», *Behavioural processes*, vol. 108, p. 183–190. [183](#)
- Krause, J., D. Hoare, S. Krause, C. Hemelrijk et D. Rubenstein. 2000, «Leadership in fish shoals», *Fish and Fisheries*, vol. 1, n° 1, p. 82–89. [182](#)
- Kurvers, R. H., B. Eijkelenkamp, K. van Oers, B. van Lith, S. E. van Wieren, R. C. Ydenberg et H. H. Prins. 2009, «Personality differences explain leadership in barnacle geese», *Animal Behaviour*, vol. 78, n° 2, p. 447–453. [181](#)
- Leblond, C. et S. G. Reebs. 2006, «Individual leadership and boldness in shoals of golden shiners (*notemigonus crysoleucas*)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [181](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [182](#)
- McClure, M., P. McIntyre et A. McCune. 2006, «Notes on the natural diet and habitat of eight danionin fishes, including the zebrafish *danio rerio*», *Journal of Fish Biology*, vol. 69, n° 2, p. 553–570. [174](#)

- Miller, N., S. Garnier, A. T. Hartnett et I. D. Couzin. 2013, «Both information and social cohesion determine collective decisions in animal groups», *Proceedings of the National Academy of Sciences*, vol. 110, n° 13, p. 5263–5268. [173](#), [183](#)
- Miller, N. et R. Gerlai. 2007, «Quantification of shoaling behaviour in zebrafish (danio rerio)», *Behavioural brain research*, vol. 184, n° 2, p. 157–166. [185](#)
- Miller, N. Y. et R. Gerlai. 2011, «Shoaling in zebrafish : what we don't know», *Reviews in the Neurosciences*, vol. 22, n° 1, p. 17–25. [185](#)
- Millot, S., M.-L. Bégout et B. Chatain. 2009, «Risk-taking behaviour variation over time in sea bass *dicentrarchus labrax* : effects of day–night alternation, fish phenotypic characteristics and selection for growth», *Journal of Fish Biology*, vol. 75, n° 7, p. 1733–1749. [181](#)
- Nakayama, S., J. L. Harcourt, R. A. Johnstone et A. Manica. 2012a, «Initiative, personality and leadership in pairs of foraging fish», *PLoS One*, vol. 7, n° 5, p. e36 606. [173](#)
- Nakayama, S., R. A. Johnstone et A. Manica. 2012b, «Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish», *PLoS One*, vol. 7, n° 8, p. e43 747. [181](#)
- Nakayama, S., A. F. Ojanguren et L. A. Fuiman. 2011, «Process-based approach reveals directional effects of environmental factors on movement between habitats», *Journal of Animal Ecology*, vol. 80, n° 6, p. 1299–1304. [173](#)
- Norton, W. et L. Bally-Cuif. 2010, «Adult zebrafish as a model organism for behavioural genetics», *BMC neuroscience*, vol. 11, n° 1, p. 1. [174](#)
- Oldroyd, B. P., R. S. Gloag, N. Even, W. Wattanachaiyingcharoen et M. Beekman. 2008, «Nest site selection in the open-nesting honeybee *apis florea*», *Behavioral Ecology and Sociobiology*, vol. 62, n° 10, p. 1643–1653. [173](#)
- Oliveira, R. F. 2014, «Mind the fish : zebrafish as a model in cognitive social neuroscience», *Frontiers in neural circuits*. [174](#)
- Parichy, D. M. 2015, «Advancing biology through a deeper understanding of zebrafish ecology and evolution», *ELife*, vol. 4, p. e05 635. [174](#)
- Parrish, J. K., S. V. Viscido et D. Grünbaum. 2002, «Self-organized fish schools : an examination of emergent properties», *The biological bulletin*, vol. 202, n° 3, p. 296–305. [173](#)
- Pearce, J. M. 2013, *Animal learning and cognition : an introduction*, Psychology Press. [173](#)
- Pérez-Escudero, A., J. Vicente-Page, R. C. Hinz, S. Arganda et G. G. de Polavieja. 2014, «idtracker : tracking individuals in a group by automatic identification of unmarked animals», *Nature methods*, vol. 11, n° 7, p. 743–748. [185](#)

- Petit, O. et R. Bon. 2010, «Decision-making processes : the case of collective movements», *Behavioural Processes*, vol. 84, n° 3, p. 635–647. [173](#)
- Pettersson, L. B. et C. Brönmark. 1993, «Trading off safety against food : state dependent habitat choice and foraging in crucian carp», *Oecologia*, vol. 95, n° 3, p. 353–357. [173](#)
- Pratt, S. C., E. B. Mallon, D. J. Sumpter et N. R. Franks. 2002, «Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *leptothorax albipennis*», *Behavioral Ecology and Sociobiology*, vol. 52, n° 2, p. 117–127. [173](#)
- Pritchard, V. L., J. Lawrence, R. K. Butlin et J. Krause. 2001, «Shoal choice in zebrafish, *danio rerio* : the influence of shoal size and activity», *Animal Behaviour*, vol. 62, n° 6, p. 1085–1088. [174](#)
- Radakov, D. V. 1973, «Schooling in the ecology of fish», . [173](#)
- Reebs, S. G. 2000, «Can a minority of informed leaders determine the foraging movements of a fish shoal?», *Animal behaviour*, vol. 59, n° 2, p. 403–409. [182](#)
- Rieucou, G., J. Morand-Ferron et L.-A. Giraldeau. 2010, «Group size effect in nutmeg mannikin : between-individuals behavioral differences but same plasticity», *Behavioral Ecology*, p. arq039. [173](#)
- Rosenthal, S. B., C. R. Twomey, A. T. Hartnett, H. S. Wu et I. D. Couzin. 2015, «Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion», *Proceedings of the National Academy of Sciences*, vol. 112, n° 15, p. 4690–4695. [173](#), [182](#)
- Séguret, A., B. Collignon, L. Cazenille, Y. Chemtob et J. Halloy. 2017, «Loose social organisation of ab strain zebrafish groups in a two-patch environment», *arXiv preprint arXiv :1701.02572*. [174](#), [181](#)
- Sison, M. et R. Gerlai. 2010, «Associative learning in zebrafish (*danio rerio*) in the plus maze», *Behavioural brain research*, vol. 207, n° 1, p. 99–104. [173](#)
- Spence, R., M. Fatema, M. Reichard, K. Huq, M. Wahab, Z. Ahmed et C. Smith. 2006, «The distribution and habitat preferences of the zebrafish in bangladesh», *Journal of Fish Biology*, vol. 69, n° 5, p. 1435–1448. [174](#)
- Spence, R., G. Gerlach, C. Lawrence et C. Smith. 2008, «The behaviour and ecology of the zebrafish, *danio rerio*», *Biological Reviews*, vol. 83, n° 1, p. 13–34. [174](#)
- Strandburg-Peshkin, A., C. R. Twomey, N. W. Bode, A. B. Kao, Y. Katz, C. C. Ioannou, S. B. Rosenthal, C. J. Torney, H. S. Wu, S. A. Levin et collab.. 2013, «Visual sensory networks and effective information transfer in animal groups», *Current Biology*, vol. 23, n° 17, p. R709–R711. [185](#)

- Sueur, C., J.-L. Deneubourg et O. Petit. 2011a, «From the first intention movement to the last joiner : macaques combine mimetic rules to optimize their collective decisions», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 278, n° 1712, p. 1697–1704. [173](#)
- Sueur, C., A. J. King, L. Conratt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C. M. Schaffner, L. Williams, D. Zinner et F. Aureli. 2011b, «Collective decision-making and fission–fusion dynamics : a conceptual framework», *Oikos*, vol. 120, n° 11, p. 1608–1617. [173](#)
- Sueur, C. et O. Petit. 2008, «Shared or unshared consensus decision in macaques?», *Behavioural Processes*, vol. 78, n° 1, p. 84–92. [182](#)
- Sumpter, D. J., J. Krause, R. James, I. D. Couzin et A. J. Ward. 2008, «Consensus decision making by fish», *Current Biology*, vol. 18, n° 22, p. 1773–1777. [183](#)
- Suriyampola, P. S., D. S. Shelton, R. Shukla, T. Roy, A. Bhat et E. P. Martins. 2016, «Zebrafish social behavior in the wild», *Zebrafish*, vol. 13, n° 1, p. 1–8. [174](#)
- Ward, A. J., J. E. Herbert-Read, L. A. Jordan, R. James, J. Krause, Q. Ma, D. I. Rubenstein, D. J. Sumpter et L. J. Morrell. 2013, «Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish», *The American Naturalist*, vol. 181, n° 6, p. 748–760. [173](#)
- Ward, A. J., J. E. Herbert-Read, D. J. Sumpter et J. Krause. 2011, «Fast and accurate decisions through collective vigilance in fish shoals», *Proceedings of the National Academy of Sciences*, vol. 108, n° 6, p. 2312–2315. [173](#), [181](#), [183](#)
- Ward, A. J., J. Krause et D. J. Sumpter. 2012, «Quorum decision-making in foraging fish shoals», *PloS one*, vol. 7, n° 3, p. e32411. [183](#)
- Ward, A. J., D. J. Sumpter, I. D. Couzin, P. J. Hart et J. Krause. 2008, «Quorum decision-making facilitates information transfer in fish shoals», *Proceedings of the National Academy of Sciences*, vol. 105, n° 19, p. 6948–6953. [183](#)
- Watts, D. 2000, «Mountain gorilla habitat use strategies and group movements», *On the move : how and why animals travel in groups*. University of Chicago Press, Chicago, IL, p. 351–374. [173](#)
- Wiens, J. A. 1976, «Population responses to patchy environments», *Annual review of ecology and systematics*, p. 81–120. [174](#)
- Wilson, A. D. et J.-G. J. Godin. 2010, «Boldness and intermittent locomotion in the bluegill sunfish, *Lepomis macrochirus*», *Behavioral Ecology*, vol. 21, n° 1, p. 57–62. [181](#)

Chapitre 10

Discussion Générale et Conclusion

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10.1 Résultats principaux

Les travaux effectués durant cette thèse ont permis d'enrichir les connaissances sur les déplacements en groupe, les comportements collectifs et la prise de décision au sein de l'espèce *Danio rerio* (zebrafish).

Comportements collectifs

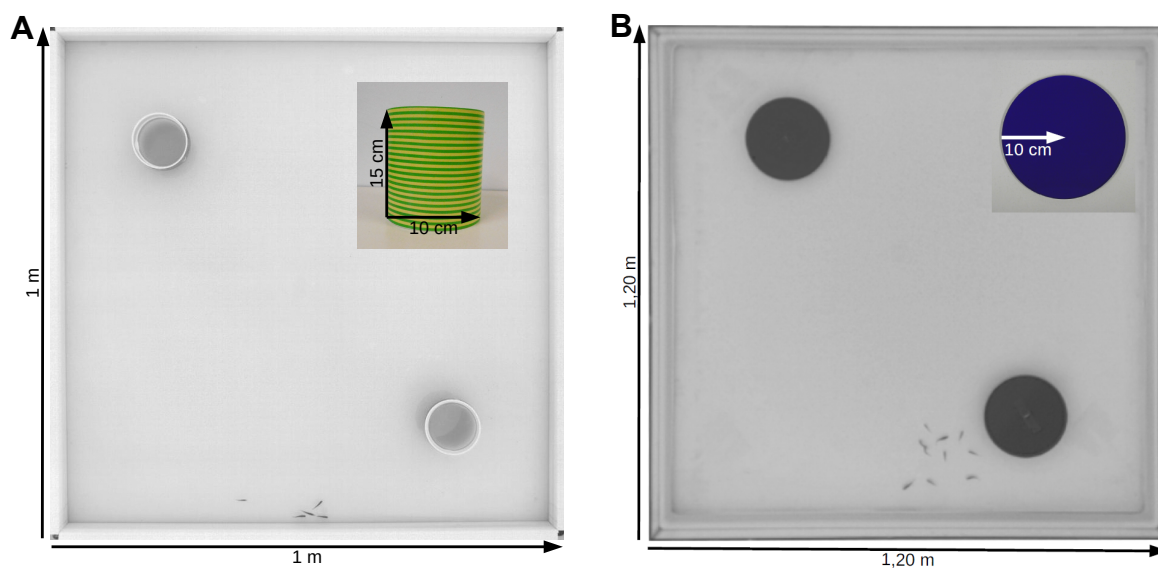


FIGURE 10.1 – Environnement ouvert et points de repère. (A) Disques flottants, (B) cylindres immergés.

Dans une première étude, nous avons testé deux tailles de population – 5 et 10 individus – chez deux souches de zebrafish aux phénotypes différents – la souche AB présente de courtes nageoires alors qu’elles sont longues chez la souche TL – dans un grand aquarium où deux points de repères identiques ont été positionnés dans la diagonale (soit des disques flottants à la surface de l’eau, soit des cylindres immergés et présents dans toute la colonne d’eau) 10.1. Tout d’abord, nous constatons que les zebrafish AB et TL sont constamment en mouvement et passent à proximité des points de repères, sans s’y arrêter. Nous révélons ensuite que les zebrafish TL sont plus cohésifs que les zebrafish AB. Aussi, l’augmentation de la taille de la population n’a pas d’effet sur la cohésion des groupes de souche TL alors qu’elle accroît fortement la cohésion des groupes de zebrafish de type AB. En terme de préférence spatiale liée aux cylindres, une série de tests ANOVA à deux facteurs et post hoc, a montré que les groupes de 10 zebrafish AB sont plus attirés par les cylindres que les groupes de 5 AB et 5 TL, eux même plus attirés que les groupes de 10 TL. De même, il ressort que les groupes de 10 zebrafish AB sont plus attirés par tout type de points de repères dans leur environnement que les groupes de 10 zebrafish TL. Enfin, nous avons montré que ces derniers (TL) préfèrent nager dans le voisinage de points de

repères immergés (cylindres) plutôt que flottants (disques).

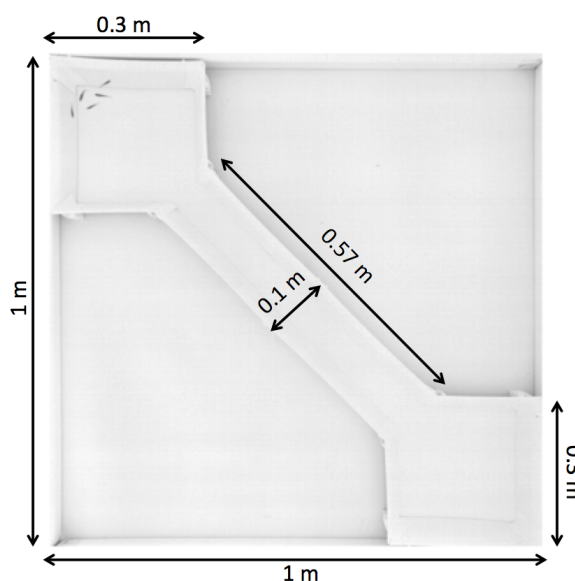


FIGURE 10.2 – Environnement contraint de type labyrinthe simple, constitué de deux salles connectées par un couloir.

Fort de ces résultats nous avons conçu une expérience de choix binaires : un "labyrinthe" très simple constitué de deux grandes salles carrées connectées par un couloir (soit trois zones) 10.2. Cette fois-ci nous n'avons testé que la souche AB pour sept tailles de populations différentes (1, 2, 3, 5, 7, 10 et 20 zebrafish). Au-delà du simple constat que les zebrafish passent d'une salle à l'autre sans interruption, nous mettons en évidence dans nos analyses que plus un groupe est important plus les distances entre les plus proches voisins s'amenuisent tandis que celles séparant chaque paire de poissons s'accroissent. Pour ce qui est de l'utilisation de l'espace, quand les zebrafish se regroupent dans une des deux salles, ils le font en groupe de plus de 80% de la population. Néanmoins, plus le groupe est grand moins on recensera d'événements de résidence collective (toute la population) dans les chambres : la médiane de ces événements passe de 233 pour des groupes de 2 poissons à 131 pour des groupes de 10 poissons.

En constatant l'intérêt que peut porter la communauté étudiant les comportements collectifs sur les labyrinthes en Y et que les zebrafish sont toujours en mouvement et transitent entre les points de repères ou les salles, nous avons décidé d'en proposer une version actualisée : un labyrinthe en Y perpétuel où chaque salle de départ est aussi une salle d'arrivée 10.3. Ici, l'expérimentateur n'intervient pas pour repositionner les animaux dans la zone de départ (comme dans toutes les expériences du domaine réalisées en labyrinthes en Y). On laisse les poissons évoluer dans le labyrinthe autant de temps qu'on veut (une heure dans nos expériences). Tout au long des vingt répliqués, les zebrafish passent de salle en salle à travers les couloirs avec un taux d'habituation très faible, y compris après une heure. En effet, en découpant nos analyses par quart d'heure, nous constatons

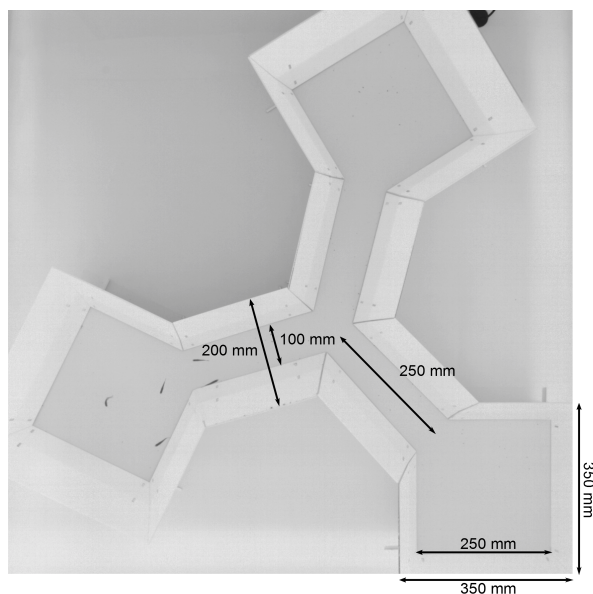


FIGURE 10.3 – Environnement contraint (fragmenté) de type labyrinthe perpétuel en Y, constitué de trois salles connectées par trois couloirs reliés entre eux.

que le nombre de transitions varie très peu avec tout de même une différence significative entre les premier et dernier quarts d'heure et que le temps de traversée des couloirs est stable pour tous les replicats.

Prise de décision

Quelque soit l'expérience, nous remarquons que pour les deux souches et toutes les tailles de population testées, aucun des groupes n'arrête son choix, à long terme, sur l'un ou l'autre repère ou salle; ils oscillent continuellement entre l'un et l'autre. En environnements contraints, tels que le système expérimental à deux chambres et le labyrinthe perpétuel en Y, nous remarquons que les groupes majoritaires (au moins 70% de la population) font 5 à 6 fois moins de demi-tours que de transitions (vers l'autre salle ou bien à droite ou à gauche, respectivement), pour des tailles de population inférieures à 10 individus. En environnement ouvert (aquarium avec des points de repère), cet écart est beaucoup plus réduit (1.5 à 3 fois moins de demi-tours).

Déplacements collectifs

Quelque soit l'expérience, l'analyse des types de transitions révèle que plus la population est grande plus les individus ont tendance à transiter en groupes restreints. Dans l'expérience du simple "labyrinthe", nous avons mesuré pour chaque poisson des sept tailles de populations testées, grâce à un nouveau système de tracking (idTracker), des constantes basiques comme les distances parcourues et les vitesses moyennes dans les trois zones. Nous remarquons que les individus seuls et les membres de grands groupes

parcourent tout au long des réplicats de petites distances et nagent moins vite. Aussi, selon la zone et pour toute population confondue, les zebrafish présentent des vitesses de déplacement très différentes : ils nagent plus lentement dans les salles.

Enfin, l'analyse des départs collectifs d'une des deux salles montre que les poissons adoptent, quelques secondes avant et au moment de la sortie, une organisation bien particulière. En effet, les zebrafish situés juste après l'initiateur du mouvement ainsi que les derniers à sortir ne changent que très rarement de position entre les quelques secondes avant la sortie du groupe et le moment effectif de la sortie. Ainsi, nous remarquons qu'il existe un lien de corrélation de plus en plus ténu entre l'ordre de sortie et le classement des distances par rapport à l'initiateur du mouvement selon que l'on se rapproche de l'instant du départ. 2 secondes avant le départ, cette corrélation oscille entre 17% et 24% selon la taille de la population et 1 seconde avant, elle s'étend de 29% à 47%. Aussi, plus le groupe est grand, moins nous comptons d'événements de départs collectifs : la médiane passant de 212 événements pour des groupes de 2 poissons à 16 pour des groupes de 10 poissons. Enfin, on remarque une corrélation positive significative pour les groupes de 5, 7 et 10 individus entre la vitesse linéaire moyenne et le nombre de tentatives de sortie effectuées par chaque individu. En affinant nos analyses, nous classons alors chaque poisson selon leurs tentatives d'initiation d'un départ collectif et leur vitesse linéaire moyenne et notons une corrélation positive pour des groupes de 3, 5, 7 et 10 individus. Ainsi, le poisson le plus rapide tout au long du réplicat est plus enclin à effectuer des départs collectifs. Ces deux résultats montrent clairement que l'initiation d'un mouvement collectif est dépendant du degré de mobilité des poissons, notamment pour les groupes denses.

Leadership

En étudiant des déplacements collectifs dans le labyrinthe simple et le labyrinthe perpétuel en Y, nous nous sommes concentrés sur la notion de leadership. Nous avons donc analysé les sorties des salles et quels en sont les initiateurs. Il ressort, pour les deux types de labyrinthes et quelque soit la taille de la population, que le leadership est généralement partagé entre les individus et que les tentatives de sortie et les initiations effectives sont proportionnellement liées. Nous remarquons aussi que certains individus ont tendance à tenter plus de sorties que d'autres. Enfin, pour le labyrinthe perpétuel en Y et en se concentrant sur les leaders principaux, nous mettons en avant l'existence d'individus super leaders (en opposition aux autres leaders) qui, dans un quart des réplicats, s'imposent pour 50% des départs collectifs. Il en est de même pour les expériences en labyrinthe simple, où l'on remarque que plus le groupe est grand moins il émerge des super leaders (pour 2 individus, dans 100% des réplicats un super leader émerge, pour 3 individus, 42%, pour 5 individus 25%, pour 7 individus, 8% et pour 10 individus, 8%).

10.2 Variations phénotypiques

Durant les premiers mois de la thèse nous nous sommes lancés dans une recherche purement prospective. [Lange et collab. \[2013\]](#), en 2013, comparent différentes souches de zebrafish et montre que les zebrafish AB et casper parcourent plus de distance dans un temps donné que d'autres de types ABstrg, EK, TU ou WIK. Aussi, [Plaut \[2000\]](#) montre que la taille des nageoires affecte les performances et comportements de nage des zebrafish. Après avoir sélectionné des points de repères dignes d'intérêts pour les deux souches de zebrafish (AB et TL) que nous souhaitions étudier, nous avons comparé leurs réactions. Comme nous l'avions rappelé plus tôt dans le chapitre 3 – Matériel et méthode –, la souche AB présente une peau zébrée et de courtes nageoires alors que la souche TL a une peau léopard et de longues nageoires. La souche AB, apparue en 1991, est issue du croisement des souches A et B. La souche TL, elle, est homozygote pour les gènes leo^{t1} , mutation récessive causant l'apparition de points sur la peau de l'adulte and lof^{dt2} responsable de l'apparition des longues nageoires [Iovine et Johnson \[2000\]](#), [Watanabe et collab. \[2006\]](#). L'intérêt de l'utilisation de ces deux souches réside dans le fait qu'elles sont toutes les deux considérées comme de type sauvage et que les deux seules différences morphologiques qui les séparent sont issues de deux mutations qui n'affectent en rien leurs capacités cognitives.

En suivant les recherches de Plaut, les remarques des spécialistes dans divers élevages de zebrafish sur Paris et notre intérêt pour les comportements collectifs, et compte tenu des moyens techniques à notre disposition durant cette période, nous nous focalisons essentiellement sur les réactions et les caractéristiques des groupes. Contre toute attente, les cohésions des groupes chez les types AB et TL sont légèrement différentes. La souche AB semble toujours moins cohésive que la souche TL et plusieurs hypothèses s'offrent à nous. Les zebrafish de la souche TL ont de longues nageoires et nous pouvons émettre alors comme hypothèse l'idée qu'ils déplacent une plus grande quantité d'eau et donc produisent un signal de présence beaucoup plus fort. Ainsi, il devient aisé pour les autres congénères de percevoir le signal via leurs lignes latérales et s'aligner les uns avec les autres. L'alignement étant plus simple, la cohésion du groupe se trouve renforcée. Pour les types AB, c'est l'inverse : de plus petites nageoires émettent un signal de présence plus faible, ce qui rend plus difficile la cohésion du groupe. Il ne faut pas oublier que la ligne latérale est généralement exploitée par les poissons afin d'établir une distance minimale entre eux (répulsion) alors que la vue est utilisée pour se rapprocher (attraction). Avec les techniques qu'on a développé depuis, il serait intéressant d'étudier précisément l'alignement des zebrafish AB et TL. L'idée serait de tester si les groupes de type TL sont plus alignés que les groupes de type AB, ce qui conforterait l'hypothèse développée ci-dessus. D'autres hypothèses ont été formulées telles que des champs visuels voire même

des lignes latérales différents entre les deux souches. Alors qu'aucune mutation décrite plus haut, à savoir leo^{t1} ou lof^{t2} , ne serait à même d'expliquer des différences dans les champs visuels, seul leo^{t1} pourrait impacter la ligne latérale, puisqu'elle touche la peau. La mutation du gène leo chez les TL aurait donc pu réduire les performances de leurs lignes latérales. Ainsi, le comportement de répulsion chez les types TL se déclencherait quand les poissons seraient beaucoup plus proches les uns des autres que ce qu'on a pu constater chez les AB. Ceci renforcerait encore la cohésion des zebrafish TL.

Chacune de ces hypothèses pourraient expliquer les différences qu'on observe entre les deux souches en matière de cohésion, et il est même possible qu'elles se complètent. Enfin, nous remarquons que les zebrafish AB sont tout autant attirés par des points de repères flottants à la surface de l'eau (disques) ou immergés dans la colonne d'eau (cylindres) alors que les types TL préfèrent clairement les cylindres aux disques. Dans la nature, on peut retrouver ces différents points de repères sous la forme de feuilles flottantes sur la surface de l'eau ou de rochers immergés. Pour l'heure nous n'avons pas d'autres explications, concernant ces préférences, que ce constat : quelque soit la souche, les zebrafish sont connus pour éviter les zones à découvert et pour suivre les bords de l'aquarium [Collignon et collab. \[2016\]](#).

10.3 Effets de la densité

Dans le premier article qui compare les deux souches AB et TL chez le zebrafish, nous esquissons l'idée d'un possible impact de la taille des population sur les comportements collectifs. En effet, nous trouvons, dans la littérature, plusieurs exemples chez diverses espèces de poissons. [Becco et collab. \[2006\]](#) avec *Oreochromis niloticus*, [Herbert-Read et collab. \[2013\]](#) chez *Gambusia holbrooki* et [Tunstrøm et collab. \[2013\]](#) pour *Notemigonus crysoleucas* montrent que la taille des populations influe sur leurs déplacements voire même leurs comportements collectifs. Les auteurs iront jusqu'à révéler des résultats opposés : plus la population d'*Oreochromis niloticus* est grande, plus les individus sont alignés entre eux; pour *Notemigonus crysoleucas* c'est une toute autre organisation qui émerge. En faisant varier la taille des populations des deux souches (5 et 10 individus), nous notons des comportements de groupe très différents : alors que les populations constituées de 10 zebrafish de type AB sont détectées plus souvent autour des points de repères que les populations de 5 zebrafish de la même souche, nous retrouvons l'opposé chez les populations de la souche TL, où les groupes de 5 individus marquent une plus grande attraction pour les points de repères.

Dès lors, la question de l'impact de la taille des populations sur les comportements collectifs chez le zebrafish s'est naturellement posée. Nous avons mis en place de nouveaux système expérimental et protocole afin de répondre à cette nouvelle question. C'est

donc dans un aquarium constitué d'un simple "labyrinthe" de type deux salles connectées par un couloir que nous avons testés les comportements collectifs et individuels chez sept tailles de population de zebrafish (1, 2, 3, 5, 7, 10 et 20 individus). Nous constatons, sans aucun doute un effet direct de la densité de la population les distances entre individus. Néanmoins, c'est dans l'étude des transitions entre les salles que nous mettons à jour les modifications des comportements collectifs impactées par la densité des populations. Dès 10 individus, le nombre de transitions collectives entre les deux salles s'effondre. Il semblerait que les groupes se divisent en sous-groupe. Cette hypothèse se confirme si on suit attentivement l'évolution de la taille des groupes et des sous-groupes se formant dans les salles. Alors que la proportion de sous-groupes est nulle pour des populations de 2 individus, qu'elle stagne autour de 2% pour des petites tailles de populations (3, 5 et 7 individus), elle atteint les 5% pour des populations de 10 individus et double quasiment (10%) quand 20 individus sont rassemblés. Chez les zebrafish, la taille des populations semble dépendre des mécanismes de fusion-fissions des groupes : plus la population est grande, plus elle sera sous-divisée. Ces mécanismes sont fréquents dans la nature; un de leurs effets est le tri des poissons en fonction de leur taille, notamment chez *Fundulus diaphanus*, *Notemigonus crysoleucas*, *Catostomus commersonii* ou encore *Poecilia reticulata* selon [Croft et collab. \[2003\]](#); [Hoare et collab. \[2000\]](#); [Krause et Ruxton \[2002\]](#). Nous n'avons pas pu mettre en évidence ce type de classement chez les zebrafish car concentrés sur d'autres interrogations, mais la question reste en suspens. Enfin, il est possible aussi, comme chez *Myotis bechsteinii*, que la fusion-fission participe d'un transfert d'information entre les différents sous-groupes; c'est d'ailleurs ce qu'ont montré [Sueur et collab. \[2011\]](#).

10.4 Prise de décision, personnalité et leadership

Les systèmes expérimentaux que nous avons mis au point ont pour objectif de montrer l'existence de mécanismes décisionnels chez le zebrafish et de mesurer l'impact du groupe sur les choix proposés. Ces systèmes expérimentaux s'inspirent de tout un pan de la recherche sur les mécanismes décisionnels. Ils sont complémentaires des labyrinthes en Y, typiques. En soumettant aux poissons zèbres deux alternatives identiques, nous focalisons alors la prise de décision non pas sur l'aspect qualitatif du choix, comme dans nombre d'études sur les comportements de décisions, mais bien sur l'impact du groupe sur le choix des individus le composant. Nous remarquons que quelque soit la souche et la taille de la population, les zebrafish ne montrent aucune préférence globale pour l'une ou l'autre alternative (après une heure par réplicat), mais balançent leurs choix de façon ponctuelle pour l'une ou l'autre. De manière surprenante et après une seule heure d'expérience, le choix d'une zone de vie par les zebrafish diffère déjà de celui de nom-

breuses espèces chez qui la fidélité spatiale émerge des interactions entre les individus et s'impose pour des temps plus longs. On pourra citer les cafards [Ame et collab. \[2004\]](#), les hyménoptères [Franks et collab. \[2002\]](#), certains crabes [Brousseau et collab. \[2002\]](#) ou poissons [Thorrold et collab. \[2001\]](#); [Wolfe et Lowe \[2015\]](#). Dès lors la compréhension des oscillations entre les différentes alternatives (disques, cylindres ou salles) et leur déclenchement devient cruciale.

10.4.1 Le groupe face aux personnalités

[Dahlbom et collab. \[2011\]](#); [Guayasamin \[2013\]](#) ont remarqué chez les zebrafish l'existence de personnalités peureuses et téméraires qui sont moteurs d'exploration dans un environnement inconnu. Les zebrafish les plus téméraires s'éloignent ainsi plus facilement du groupe tout en favorisant les transitions vers une autre zone d'intérêt. Ce comportement a déjà été mis en avant par [Harcourt et collab. \[2009\]](#); [Ward et collab. \[2004\]](#) chez *Gasterosteus aculeatus* et [Leblond et Reeb \[2006\]](#) ont remarqué que des groupes de *Notemigonus crysoleucas* peureux initiaient moins de transitions que des groupes téméraires. Enfin, chez les mammifères aussi, les personnalités peureuses et téméraires sont des modificateurs de comportements collectifs : [Michelena et collab. \[2009\]](#) remarquaient que les moutons les plus téméraires avaient tendance à séparer les groupes en sous-groupes de tailles égales. En se re-concentrant sur nos résultats chez le zebrafish, on assiste, lors des transitions entre les zones d'intérêts, à des événements essentiels qui pourraient achever de justifier l'impact des personnalités sur le groupe. Nous avons appelé ces types de transitions les un-à-un (One-by-one) et les demi-tours (U-turn). Durant ces premières, les plus rares, les poissons transitent les uns après les autres et ce une fois que le précédent poisson a atteint la zone d'intérêt. Les deuxièmes se déroulent quand le groupe, déjà lancé pour atteindre l'autre zone d'intérêt, décide de revenir à son point de départ. Quelque soit le type de système expérimental, on en recense 5 à 6 fois moins que les transitions typiques, en groupe. Comme on peut le comprendre très facilement, dans un contexte naturel avec son lot de prédateurs, les transitions un-à-un sont extrêmement périlleuses : les poissons y sont très exposés et nous pourrions associer ces transitions à des événements téméraires. Quant aux demi-tours, il est fort possible de les assimiler à des événements peureux. Finalement, une dernière chose marquante a été de constater que les souches AB et TL ne sont pas égales face aux transitions. Bien que l'une et l'autre transitent de la même façon entre les zones d'intérêt, nous remarquons tout même que la souche AB présente plus d'événements de transitions de type un-à-un et moins de demi-tours que la souche TL.

Néanmoins, la personnalité n'est pas qu'une affaire de témérité. Dans leur article traitant des déplacements collectifs de *Gambusia holbrooki*, [Herbert-Read et collab. \[2013\]](#)

ont mis en avant le fait que ces poissons vont jusqu'à se conformer au comportement du groupe auquel ils appartiennent, en copiant les mouvements de leurs voisins congénères. Dans ce cas, les personnalités individuelles s'effacent au profit du comportement du groupe. Pour autant, dans certains contextes sociaux, *Gambusia holbrooki*, *Perca wivaltis* et *Gasterosteus aculeatus* maintiennent, tout de même, certains traits comportementaux individuels [Burns et collab. \[2012\]](#); [Magnhagen et Bunnefeld \[2009\]](#); [Nakayama et collab. \[2012\]](#). Ce type de changement de personnalité n'est pas que l'apanage des poissons puisque certains oiseaux (*Erythrura gouldiae*) sont connus pour ajuster leurs comportements aux personnalités de leurs partenaires [King et collab. \[2015\]](#).

Enfin, qu'est la personnalité sans l'existence des interactions préférentielles? Dans l'étude des comportements collectifs des zebrafish parmi sept tailles de populations, en environnement morcelé (un couloir connectant deux salles), nous constatons l'existence de paires affines entre les différents poissons. En effet, certains couples semblent beaucoup plus cohésifs que d'autres. D'ailleurs, [Briard et collab. \[2015\]](#); [King et collab. \[2011\]](#); [Sueur et Petit \[2008\]](#); [Sueur et collab. \[2009\]](#) ont remarqué que les affinités se retrouvent chez d'autres espèces, des chevaux domestiques aux primates (*Macaca mulatta*, *Macaca tonkeana* ou encore *Papio ursinus*) et jouent un rôle majeur dans les mouvements collectifs.

10.4.2 Leadership

Comme nous en parlions dans l'introduction de cette thèse, le leadership est très répandu dans le monde animal mais est très variable. Les systèmes expérimentaux de type labyrinthe correspondent parfaitement aux types d'analyses que nous souhaitons mener sur le leadership. Souvenons-nous en, le leadership a été défini par [Krause et collab. \[2000\]](#) comme l'initiation de nouvelles directions de locomotions suivies par les autres membres du groupe et complété par [Bourjade et collab. \[2015\]](#) : le leadership se réfère aux individus qui mènent le groupe plus souvent que d'autres, sur le long terme.

Départs collectifs

Ainsi, notre système expérimental favorise les transitions entre différentes zones par l'intermédiaire d'un couloir soit autant d'initiations de nouvelles directions de locomotions. D'ailleurs [Bourjade et collab. \[2009\]](#) utilisent des contraintes territoriales similaires, en milieu extérieur, quand ils étudient les comportements de pré-départ et les départs collectifs chez *Equus ferus przewalskii*. Nous avons vu plus haut que la très grande majorité des transitions se déroulait en groupe, d'où l'intérêt de comprendre ce qui pousse les individus à initier un départ d'une salle et à sortir tous ensemble. Au-delà de la simple personnalité de chaque individu (par exemple la témérité, la peur, etc.) nous remarquons

que les zebrafish adoptent une organisation bien définie lors d'événements de départ collectif. [Ward et collab. \[2013\]](#) ont montré que chez les groupes de 5 individus de *Dascyllus aruanus* se sont généralement les individus les plus proches de l'initiateur qui le suivront et que la fréquence d'égalité entre le rang de sortie et le rang de distance d'un poisson par rapport à l'initiateur décroît plus le rang de sortie est grand. Pour information, l'égalité est retrouvée dans 53% des départs pour un poisson classé 2^{ème} mais chute à 3.5% pour une 5^{ème} position. Chez le zebrafish de type AB, cette organisation diffère légèrement. Nous avons testé quatre tailles de population (3, 5, 7 et 10 individus) pour douze réplicats chacune. Nous observons que pour 75 à 90% des départs collectifs, les poissons classés 2^{ème} sont aussi les plus proches de l'initiateur, pour le rang 3, la fréquence oscille de 50 à 65%. Malheureusement, pour les autres rangs, la fréquence ne varie presque plus en fonction du rang de sortie. Néanmoins, il existe pour le dernier poisson à sortir, une tendance qui se démarque du lots des autres rangs (hormis 2 et 3) : dans 38 à 75% des départs collectifs, le dernier poisson à sortir est aussi le poisson le plus loin de l'initiateur. Toutes ces différences avec *Dascyllus aruanus* nous ont poussé à regarder ce qu'il se passait avant le départ collectif. L'analyse des rang de sortie et rang des distances par rapport à l'initiateur en fonction du temps avant et pendant la sortie montre une très forte corrélation à l'instant du départ (60 à 80%), une forte corrélation 1 seconde avant le départ (30 à 50%) et même une corrélation moindre 2 secondes avant (18 à 25%). Ces résultats viennent apporter de nouvelles informations quant à l'organisation du groupe avant et pendant un départ collectif. Nous savions déjà, grâce à [Rosenthal et collab. \[2015\]](#), que dans les populations de *Notemigonus crysoleucas*, l'initiateur est le poisson le plus excentré du groupe dans 27% des cas et que le premier à répondre au comportement de l'initiateur est le deuxième poisson le plus excentré, à un moment où la densité du groupe est faible. De plus, on voit encore le même phénomène chez d'autres espèces, chez *Gasterosteus aculeatus*, tout comme *Ovis aries*, un individu excentré peut initier un départ collectif ([Leblond et Reeb \[2006\]](#); [Pillot et collab. \[2010\]](#)). Enfin, l'enchaînement des sorties des zebrafish est non sans rappeler l'idée d'une cascade de changements de comportements développée aussi par [Rosenthal et collab. \[2015\]](#). Comme nous avons pu le voir ci-dessus, il existe clairement entre les espèces des invariants lors des départs collectifs. Finalement, tous ces départs sont initiés par un individu qui a choisit de se déplacer mais dont l'action a influencé le groupe en entier.

Un leadership partagé

[Leca et collab. \[2003\]](#); [Petit et collab. \[2009\]](#), en observant des populations de *Cebus capucinus*, dénotent des comportements qui se synchronisent dès lors qu'un des membres du groupe se déplace. En revanche, la synchronisation n'a lieu que si une fraction minimale de la population est engagée dans le processus avec l'initiateur. C'est ce que nous

tentons d'observer chez le zebrafish. Dans les deux labyrinthes précédemment décrits, nous définissons les leaders comme des initiateurs de sortie de salle suivis par un nombre minimal d'individus. Quoi qu'il en soit, chez les zebrafish, l'initiation d'un départ collectif est partagée entre tous les individus. Néanmoins, il existe de grandes disparités quant à la distribution du rôle de l'initiateur : certains zebrafish dirigent le groupe plus souvent que d'autres (super leaders).

Nous avons vu, plus haut, que la personnalité a un impact direct sur la propension des zebrafish et autres espèces à visiter leur environnement. Il se pourrait qu'un lien existe entre le leadership et la personnalité. Pour établir ce lien, il faut garder à l'esprit la définition de Krause complétée par Bourjade. Quelques auteurs ont déjà suggéré cette idée (Burns et collab. [2012]; Kurvers et collab. [2009]) tout en notant que les animaux les plus actifs sont ceux qui tentent le plus d'initier un départ collectif. C'est d'ailleurs le sujet d'un article que nous préparons mais qui ne sera pas dévoilé dans cette thèse.

Nous constatons, dans des environnements morcelés, que l'organisation des groupes de zebrafish tend en général vers un leadership partagé et que ces poissons nagent essentiellement ensemble tout en transitant sans interruption entre les salles. Par ailleurs, nous débutons une étude qui a pour objectif de caractériser les oscillations, des groupes de zebrafish, entre les deux salles. Nos premiers résultats montrent que, pour des groupes de 5 individus, les oscillations sont non-périodiques. Nous sommes actuellement en train de développer nos analyses pour différentes densités de populations (1, 3 et 7 individus). Nous pensons que la non-périodicité des oscillations est un facteur dépendant directement de l'organisation sociale des zebrafish. Par la même occasion, nous nous demandons si le leadership présenté par les zebrafish est indispensable. En effet, si le leadership n'avait pas été essentiel dans la prise de décision du zebrafish, nous aurions pu imaginer des oscillations périodiques entre les chambres. Le fait de tester des individus seuls permettrait de répondre à cette interrogation.

10.5 Le zebrafish ou le parjure de la généralisation ?

Ainsi, cette recherche prospective des mouvements collectifs et de la structure sociale chez le zebrafish, *Danio rerio*, dans des environnements ouverts ou fragmentés nous a permis de mettre en évidence des différences notables de comportements de groupe selon les souches, les densités de population et les milieux de vie testés. Nos résultats suggèrent que les comportements collectifs ne peuvent ni être généralisés à toutes les espèces ni au sein même des espèces, même si les animaux sociaux, en général, partagent bon nombre d'invariants, tels que l'interattraction, la coopération, le partage de l'information, les déplacements collectifs. Ainsi, les zebrafish de type AB, en opposition à ceux de type TL, en environnement ouvert, sont à la fois moins cohésifs tout en marquant des

préférences pour se regrouper dans des zones bien particulières, définies par leur environnement. La densité de la population a un effet direct sur la propension des zebrafish de type AB à se regrouper autour de ces zones, alors que son effet est contraire pour les zebrafish de type TL. En environnement contraint (labyrinthes), les groupes de zebrafish de type AB modulent l'occupation collective des salles en fonction de la densité de leur population. Il existe aussi des disparités quant au leadership, qui peut être distribué ou beaucoup moins partagé selon les groupes étudiés. De même, faire varier la densité des populations a un impact direct sur la distribution du leadership.

On comprend alors que plus on creuse les questions relatives aux comportements collectifs chez le zebrafish, tout en comparant l'état de l'art chez d'autres espèces, moins il est possible de dégager des principes généraux. Ainsi, notre recherche se doit d'être personnalisée et personnalisable. Il devient alors nécessaire de trouver des nouvelles méthodes d'analyses et de quantifier au plus près les comportements et autres interactions. Ces nouveaux moyens peuvent s'inscrire dans l'utilisation de robots qui interagissent en direct avec les animaux, d'environnements adaptatifs se mouvant au gré des comportements des sujets, etc.

10.6 Perspectives

Cette thèse s'inscrit donc dans une démarche de recherche prospective qui a pour but d'alimenter les connaissances sur les comportements individuels et collectifs du zebrafish. En rappelant le contexte de la thèse, à savoir, intégrée au sein d'un projet de recherche européen qui ambitionne de faire interagir deux espèces vivant dans des environnements et des milieux différents (*Danio rerio* et *Apis mellifera*), par l'intermédiaire de robots, nous comprenons alors son enjeu. Une partie des résultats obtenus a déjà été implémentée dans les robots que nous utilisons afin de constituer une société mixte de poissons et de robots. Aussi, la modélisation des comportements des zebrafish et le paramétrage des robots, étant des étapes lourdes dans le processus de création d'une société animale-robot, nous développons et testons les systèmes expérimentaux (points de repères, labyrinthes, etc.) avec des populations de poissons, tout en gardant à l'esprit que des robots pourraient se joindre à elles. Une fois l'environnement amélioré et validé, car répondant à des problématiques biologiques et comportementales, les informations nécessaires sont implémentées dans le modèle. Ainsi, le modèle de comportement des robots prend en compte : un modèle de perception et un modèle de déplacement qui dépendent de l'environnement (environnement ouvert, centre, bords et coins, couloir et salles). Le modèle de perception s'appuie sur les données des groupes de zebrafish recueillies lors des expériences dans les différents systèmes (points de repères et labyrinthes) : organisation du groupe, distances inter-individuelles, déplacement collec-

tif, fusion-fission des groupes, préférence, champs de vision, tentatives et initiation de départs collectifs, etc. Celui du déplacement a été monté à partir des données individuelles mesurées lors de ces mêmes expériences : vitesse instantanée, accélérations positive et négative, vitesse angulaire, etc. L'utilisation de robots a pour objectif de tester la puissance et l'efficacité des modèles développés à partir de données recueillies lors des expériences. C'est leur totale intégration dans la société animale qui nous permettra de confirmer ce point.

À plus long terme et au vu des technologies utilisées pour analyser et comprendre les comportements collectifs chez les animaux, des résultats obtenus dans cette thèse et des idées développées dans la littérature aujourd'hui, il apparaît de plus en plus évident que la personnalité de chaque membre d'une population influe sur le comportement de ladite population. Il a été suggéré que certains individus plus téméraires que d'autres initient plus facilement des départs collectifs [Harcourt et collab. \[2009\]](#), néanmoins nous ne savons pas comment ce trait de personnalité émerge, ni quels en sont les degrés. On peut même se demander s'il n'en existe pas d'autres, qui de l'altruiste partageant l'information, qui de l'exclu du groupe ou du simple suiveur. C'est d'ailleurs le sujet d'une étude que nous préparons actuellement.

Comme nous l'avons vu, le challenge développé par le projet Assisi est de faire interagir des espèces sociales de milieux différents par l'intermédiaire de robots. Néanmoins, il soulève des interrogations sur les comportements collectifs et les stratégies de cohabitation dans des populations naturellement mixtes ou non. C'est ce que nous appelons les comportements collectifs multi-espèce. De part ses dimensions et son total contrôle (qualité de l'eau, température, luminosité, isolement), nous avons réussi à créer en laboratoire un environnement propice à l'accueil de multiples espèces de poissons de petites tailles, possiblement épuré mais toujours proche de leurs milieux de vie. Dans cet environnement modulable, au gré des hypothèses que nous émettons, nous avons toujours respecté la tranquillité de nos hôtes, les scrutant sans intrusion dans leur vie, leur laissant une très grande liberté dans leurs actes individuels comme collectifs. Nous pouvons dès lors penser à constituer des sociétés mixtes d'espèces se cotoyant ou non dans la nature et relever, décrire et comprendre les indices révélateurs des interactions d'entraide, de domination ou de protection et pourquoi pas de structures sociales émergentes.

10.7 Références

- Ame, J.-M., C. Rivault et J.-L. Deneubourg. 2004, «Cockroach aggregation based on strain odour recognition», *Animal behaviour*, vol. 68, n° 4, p. 793–801. [207](#)
- Becco, C., N. Vandewalle, J. Delcourt et P. Poncin. 2006, «Experimental evidences of a structural

- and dynamical transition in fish school», *Physica A : Statistical Mechanics and its Applications*, vol. 367, p. 487–493. [205](#)
- Bourjade, M., B. Thierry, M. Hausberger et O. Petit. 2015, «Is leadership a reliable concept in animals? an empirical study in the horse», *PloS one*, vol. 10, n° 5, p. e0126344. [208](#)
- Bourjade, M., B. Thierry, M. Maumy et O. Petit. 2009, «Decision-making in przewalski horses (*equus ferus przewalskii*) is driven by the ecological contexts of collective movements», *Ethology*, vol. 115, n° 4, p. 321–330. [208](#)
- Briard, L., C. Dorn et O. Petit. 2015, «Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses», *Ethology*, vol. 121, n° 9, p. 888–902. [208](#)
- Brousseau, D. J., J. A. Baglivo, A. Filipowicz, L. Sego et C. Alt. 2002, «An experimental field study of site fidelity and mobility in the asian shore crab, *hemigrapsus sanguineus*», *Northeastern Naturalist*, vol. 9, n° 4, p. 381–390. [207](#)
- Burns, A. L., J. E. Herbert-Read, L. J. Morrell et A. J. Ward. 2012, «Consistency of leadership in shoals of mosquitofish (*gambusia holbrooki*) in novel and in familiar environments», *PLoS One*, vol. 7, n° 5, p. e36567. [208](#), [210](#)
- Collignon, B., A. Séguret et J. Halloy. 2016, «A stochastic vision-based model inspired by zebrafish collective behaviour in heterogeneous environments», *Royal Society open science*, vol. 3, n° 1, p. 150473. [205](#)
- Croft, D., B. Arrowsmith, J. Bielby, K. Skinner, E. White, I. D. Couzin, A. Magurran, I. Ramnarine et J. Krause. 2003, «Mechanisms underlying shoal composition in the trinidadian guppy, *poecilia reticulata*», *Oikos*, vol. 100, n° 3, p. 429–438. [206](#)
- Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström et S. Winberg. 2011, «Boldness predicts social status in zebrafish (*danio rerio*)», *PLoS One*, vol. 6, n° 8, p. e23565. [207](#)
- Franks, N. R., S. C. Pratt, E. B. Mallon, N. F. Britton et D. J. Sumpter. 2002, «Information flow, opinion polling and collective intelligence in house-hunting social insects», *Philosophical Transactions of the Royal Society of London B : Biological Sciences*, vol. 357, n° 1427, p. 1567–1583. [207](#)
- Guayasamin, O. 2013, «Personality matters : A quantitative comparison of asocial and social behaviors in the zebrafish (*danio rerio*)», . [207](#)
- Harcourt, J. L., G. Sweetman, R. A. Johnstone et A. Manica. 2009, «Personality counts : the effect of boldness on shoal choice in three-spined sticklebacks», *Animal Behaviour*, vol. 77, n° 6, p. 1501–1505. [207](#), [212](#)
- Herbert-Read, J. E., S. Krause, L. Morrell, T. Schaerf, J. Krause et A. Ward. 2013, «The role of individuality in collective group movement», dans *Proc. R. Soc. B*, vol. 280, The Royal Society, p. 20122564. [205](#), [207](#)

- Hoare, D., J. Krause, N. Peuhkuri et J.-G. Godin. 2000, «Body size and shoaling in fish», *Journal of Fish Biology*, vol. 57, n° 6, p. 1351–1366. [206](#)
- Iovine, M. K. et S. L. Johnson. 2000, «Genetic analysis of isometric growth control mechanisms in the zebrafish caudal fin», *Genetics*, vol. 155, n° 3, p. 1321–1329. [204](#)
- King, A. J., C. Sueur, E. Huchard et G. Cowlshaw. 2011, «A rule-of-thumb based on social affiliation explains collective movements in desert baboons», *Animal Behaviour*, vol. 82, n° 6, p. 1337–1345. [208](#)
- King, A. J., L. J. Williams et C. Mettke-Hofmann. 2015, «The effects of social conformity on gouldian finch personality», *Animal Behaviour*, vol. 99, p. 25–31. [208](#)
- Krause, J., D. Hoare, S. Krause, C. Hemelrijk et D. Rubenstein. 2000, «Leadership in fish shoals», *Fish and Fisheries*, vol. 1, n° 1, p. 82–89. [208](#)
- Krause, J. et G. D. Ruxton. 2002, *Living in groups*, Oxford University Press. [206](#)
- Kurvers, R. H., B. Eijkelenkamp, K. van Oers, B. van Lith, S. E. van Wieren, R. C. Ydenberg et H. H. Prins. 2009, «Personality differences explain leadership in barnacle geese», *Animal Behaviour*, vol. 78, n° 2, p. 447–453. [210](#)
- Lange, M., F. Neuzeret, B. Fabreges, C. Froc, S. Bedu, L. Bally-Cuif et W. H. Norton. 2013, «Inter-individual and inter-strain variations in zebrafish locomotor ontogeny», *PloS one*, vol. 8, n° 8, p. e70 172. [204](#)
- Leblond, C. et S. G. Reeb. 2006, «Individual leadership and boldness in shoals of golden shiners (notemigonus crysoleucas)», *Behaviour*, vol. 143, n° 10, p. 1263–1280. [207](#), [209](#)
- Leca, J.-B., N. Gunst, B. Thierry et O. Petit. 2003, «Distributed leadership in semifree-ranging white-faced capuchin monkeys», *Animal Behaviour*, vol. 66, n° 6, p. 1045–1052. [209](#)
- Magnhagen, C. et N. Bunnefeld. 2009, «Express your personality or go along with the group : what determines the behaviour of shoaling perch?», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1671, p. 3369–3375. [208](#)
- Michelena, P., A. M. Sibbald, H. W. Erhard et J. E. McLeod. 2009, «Effects of group size and personality on social foraging : the distribution of sheep across patches», *Behavioral Ecology*, vol. 20, n° 1, p. 145–152. [207](#)
- Nakayama, S., R. A. Johnstone et A. Manica. 2012, «Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish», *PLoS One*, vol. 7, n° 8, p. e43 747. [208](#)
- Petit, O., J. Gautrais, J.-B. Leca, G. Theraulaz et J.-L. Deneubourg. 2009, «Collective decision-making in white-faced capuchin monkeys», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 276, n° 1672, p. 3495–3503. [209](#)

- Pillot, M. H., J. Gautrais, J. Gouello, P. Michelena, R. Bon et collab.. 2010, «Moving together : Incidental leaders and naïve followers», *Behavioural Processes*, vol. 83, n° 3, p. 235–241. [209](#)
- Plaut, I. 2000, «Effects of fin size on swimming performance, swimming behaviour and routine activity of zebrafish *danio rerio*», *Journal of Experimental Biology*, vol. 203, n° 4, p. 813–820. [204](#)
- Rosenthal, S. B., C. R. Twomey, A. T. Hartnett, H. S. Wu et I. D. Couzin. 2015, «Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion», *Proceedings of the National Academy of Sciences*, vol. 112, n° 15, p. 4690–4695. [209](#)
- Sueur, C., J.-L. Deneubourg et O. Petit. 2011, «From the first intention movement to the last joiner : macaques combine mimetic rules to optimize their collective decisions», *Proceedings of the Royal Society of London B : Biological Sciences*, vol. 278, n° 1712, p. 1697–1704. [206](#)
- Sueur, C. et O. Petit. 2008, «Organization of group members at departure is driven by social structure in macaca», *International Journal of Primatology*, vol. 29, n° 4, p. 1085–1098. [208](#)
- Sueur, C., O. Petit et J.-L. Deneubourg. 2009, «Selective mimetism at departure in collective movements of macaca tonkeana : an experimental and theoretical approach», *Animal Behaviour*, vol. 78, n° 5, p. 1087–1095. [208](#)
- Thorrold, S. R., C. Latkoczy, P. K. Swart et C. M. Jones. 2001, «Natal homing in a marine fish meta-population», *Science*, vol. 291, n° 5502, p. 297–299. [207](#)
- Tunstrøm, K., Y. Katz, C. C. Ioannou, C. Huepe, M. J. Lutz et I. D. Couzin. 2013, «Collective states, multistability and transitional behavior in schooling fish», *PLoS Comput Biol*, vol. 9, n° 2, p. e1002915. [205](#)
- Ward, A. J., J. E. Herbert-Read, L. A. Jordan, R. James, J. Krause, Q. Ma, D. I. Rubenstein, D. J. Sumpter et L. J. Morrell. 2013, «Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish», *The American Naturalist*, vol. 181, n° 6, p. 748–760. [209](#)
- Ward, A. J., P. Thomas, P. J. Hart et J. Krause. 2004, «Correlates of boldness in three-spined sticklebacks (*gasterosteus aculeatus*)», *Behavioral Ecology and Sociobiology*, vol. 55, n° 6, p. 561–568. [207](#)
- Watanabe, M., M. Iwashita, M. Ishii, Y. Kurachi, A. Kawakami, S. Kondo et N. Okada. 2006, «Spot pattern of leopard danio is caused by mutation in the zebrafish connexin41. 8 gene», *EMBO reports*, vol. 7, n° 9, p. 893–897. [204](#)
- Wolfe, B. W. et C. G. Lowe. 2015, «Movement patterns, habitat use and site fidelity of the white croaker (*genyonemus lineatus*) in the palos verdes superfund site, los angeles, california», *Marine environmental research*, vol. 109, p. 69–80. [207](#)