UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA SÉLECTION DE L'ALTRUISME AU SEIN DES PETITS GROUPES : UNE APPROCHE SCIENTIFIQUE ET BIOLOGIQUE DES JEUX VIDÉO

THÈSE

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DÉDICACE

Au million de sacrifices et au soutien empathique de Eve…

à l'appui indéfectible de mes parents…

et enfin, à mes enfants, mes trois meilleurs chapitres.

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RÉSUMÉ

Les comportements altruistes génèrent un coût pour l'acteur, mais bénéficient à un autre individu, le récepteur. Des mécanismes évolutifs sont donc nécessaires pour que des comportements altruistes persistent, comme la sélection de la parentèle ou la réciprocité. L'organisation sociale est une composante essentielle dans la sélection de la plupart de ces mécanismes. La présente thèse s'intéresse à l'altruisme au sein de petits groupes. Plus spécifiquement, la familiarité entre les membres de mêmes groupes, la sélection de l'altruisme ainsi que la variation des comportements altruistes sont au cœur des interrogations des prochains chapitres. Pour étudier l'altruisme dans les petits groupes, j'utilise les jeux vidéo comme système de recherche. Les jeux vidéo, surtout multijoueurs, ont l'avantage de représenter des écosystèmes complexes, où les joueurs ont, entre eux, des interactions écologiques : prédation, compétition, coopération. Plus spécifiquement, le jeu vidéo *Dead by Daylight* est tout indiqué pour tester mes hypothèses. *Dead by Daylight* est un jeu d'horreur, où un groupe de quatre proies affronte un prédateur. Les proies doivent collectivement acquérir assez de ressources pour activer les sorties et survivre, tout en évitant de se faire capturer par le prédateur. Les proies peuvent manifester un comportement altruiste en secourant une autre proie capturée avant qu'elle soit éliminée de la partie.

En premier lieu, j'ai investigué comment la familiarité entre les proies (joueurs amis *vs* joueurs étrangers) impacte indirectement la survie via des comportements comme éviter le prédateur, acquérir des ressources, et secourir les proies capturées. Mes observations ont révélé que les proies dans les groupes plus familiers (fréquence élevée d'amis) acquéraient plus de ressources, mais rencontraient le prédateur plus souvent. Aussi, elles secouraient d'autres proies capturées plus souvent que les proies avec moins d'individus familiers dans leurs groupes. L'analyse a aussi révélé que l'altruisme avait un effet net négatif sur la survie. J'ai pu conclure que la familiarité avait un effet positif très faible sur la survie, et cela était dû à des effets indirects opposés via les comportements étudiés.

En deuxième lieu, j'ai voulu identifier et départager les différents coûts et bénéfices de l'altruisme. Pour ce faire, j'ai conçu une expérience où j'ai fixé un phénotype pur d'altruisme chez les proies (des altruistes vs des non-altruistes) pour un sous-échantillon de joueurs. Les altruistes rencontraient le prédateur plus souvent et acquéraient moins de ressources. Cependant, les altruistes permettaient de sauver des proies et ainsi garder le groupe entier plus longtemps. La taille de groupe plus grande permettait à chaque proie d'amasser des ressources plus rapidement et de réaliser des sauvetages plus facilement. Globalement, les altruistes avaient des probabilités de survie plus faibles que les non-altruistes, mais les probabilités de survie de tous augmentaient avec la fréquence d'altruistes dans le groupe. J'ai donc détecté une sélection au niveau du groupe pour l'altruisme dans notre système. Ce résultat met aussi l'emphase sur l'importance de l'hypothèse de l'augmentation de groupe pour la sélection de l'altruisme.

En dernier lieu, j'ai mesuré la proportion de la variation dans le comportement altruiste qui se situe dans les différences entre les individus (variation interindividuelle) et au fil de la vie d'un individu (variation intra-individuelle). Il n'y avait que peu de différences de niveaux d'altruisme entre les proies, mais une très grande variation intra-individuelle. L'altruisme des autres diminuait directement l'altruisme d'une proie. Nos observations contredisaient l'hypothèse de la réciprocité généralisée qui stipule que les proies « paient au suivant ». De plus, les proies en général, n'étaient pas réceptives à la rétroaction positif d'avoir survécues tout en ayant aidé dans la partie précédente, pour adapter leur niveau d'altruisme. Cette thèse inclut cinq chapitres et trois approches différentes pour comprendre davantage comment la structure en petits groupes peut affecter la sélection de l'altruisme.

Mots clés : Altruisme, coopération, jeux vidéo, sélection de groupe, prédation, familiarité, variation intra et interindividuelle

ABSTRACT

Altruistic behaviours incur a cost to the actor but benefit another individual, the receptor. Evolutionary mechanisms, like kin selection or reciprocity, are capital for costly altruistic behaviours to persist under natural selection. The social organization is a capital component in many of those mechanisms. This thesis tackles altruism among small groups. The familiarity between group members, the selection of altruism and the variation in altruism are central in the upcoming chapters. To measure altruism in small groups, I use a video game as a study system. Nowadays, multiplayer video games represent complex ecosystems where players display ecologically relevant behaviours like predation, cooperation, and competition. Specifically, the video game *Dead by Daylight* is perfect to test my hypotheses. *Dead by Daylight* is a horror game where groups of four prey face a predator. Prey must collectively gather resources to enable the exits to survive while avoiding getting captured by the predator. Prey can express altruism by rescuing captured prey before they get eliminated from the game.

First, I investigated how familiarity between prey (friends vs strangers) indirectly impacted survival via behaviours like avoiding the predator, acquiring resources and rescuing others. My observations have revealed that prey in more familiar groups (higher frequency of friends) acquired more resources but encountered the predator more often. Also, they rescued captured prey more often than prey with less familiar group members. Data also revealed that altruism had a negative impact on survival. The path analysis concluded that familiarity had a slight positive effect on survival through opposed indirect effects via other behaviours.

Second, I identified and untangled the different costs and benefits of altruism. To do so, I designed an experiment in which I fixed pure altruistic phenotypes (altruists vs non-altruists) for a subset of players. Altruists encountered the predator more often and acquired less resources than non-altruistic prey. However, altruists could save other prey and so could prevent the group from diminishing in size for longer. Larger group size allowed all prey to acquire resources faster and perform more rescues. Overall, altruistic prey had a lower survival, but the survival of all group members increased with the frequency of altruists in the group. Thus, I have detected a selection at the level of the group for altruism in our system. The study also emphasizes the importance of the group augmentation hypothesis as a selection mechanism for altruism.

Last, I measured the proportion of variation in altruism that happens among and within individuals. There was little difference in altruism among prey, but a very high within-individual variation. The altruism level of a prey was directly limited by altruism from others. Our data contradicted the generalized reciprocity hypothesis in which prey would “pay it forward”. Moreover, prey were generally not receptive to positive feedback of their own previous behaviour and did little to adapt their altruistic behaviour accordingly. Three research questions led to three different approaches to understand better how small groups can impact altruism.

Keywords: Altruism, cooperation, video games, group selection, predation, familiarity, among and within variation

CHAPITRE 1

Introduction générale

Dans la nature, l'altruisme existe sous maintes formes et au sein de plusieurs taxons. Des chiens de prairie (*Cynomys leucurus*) avertissent leurs conspécifiques en cas de présence de prédateur (Hoogland, 1979). Des cichlidés subordonnés (*Neolamprologus pulcher*) investissent du temps dans la reproduction du couple dominant (Taborsky, 2016). Des chimpanzés (*Pan troglodytes*) se partagent différents rôles pour chasser en groupe (Boesch, 2002). Des moineaux domestiques (*Passer domesticus*) appellent des conspécifiques pour partager leurs parcelles de nourriture (Elgar, 1986). Toutefois, de tels comportements altruistes chez les animaux sont un casse-tête évolutif. Un comportement dit coopératif nécessite un coût pour l'acteur (diminution de la survie ou de la reproduction), mais génère un bénéfice pour un récepteur. Ainsi défini, un tel comportement ne subsisterait pas sous l'effet de la sélection naturelle. En fait, des mécanismes évolutifs qui permettent de générer des bénéfices à l'acteur sont essentiels pour la persistance de l'altruisme (Axelrod et Hamilton, 1981).

Historiquement, la sélection de la parentèle est une des premières hypothèses à avoir été proposée (Hamilton, 1964). La sélection de la parentèle permet de sélectionner des comportements qui bénéficient à des individus apparentés, donc ceux avec qui l'acteur partage des gènes. La célèbre règle de Hamilton (1964) $br>c$ stipule qu'un comportement altruiste peut être sélectionné si les bénéfices pour le receveur (b) s par le degré de parenté (r) sont plus grands que les coûts pour l'acteur (c). Ainsi, de tels comportements, quoique coûteux pour l'acteur, ne vont plus à l'encontre de l'évolution, car ils améliorent indirectement l'aptitude phénotypique de l'acteur (l'aptitude indirecte, Hamilton, 1964). Pendant des décennies, la sélection de parentèle et l'aptitude indirecte restaient l'explication principale pour la sélection de l'altruisme, surtout pour les colonies d'insectes sociaux (Foster *et al.*, 2006). Le soutien empirique pour la sélection de parentèle est abondant (Browning *et al.*, 2012 ; Kingma *et al.*, 2011 ; Riehl, 2017).

La réciprocité est une autre hypothèse qui a éclipsé les autres dans la littérature scientifique pendant une longue période et suppose que le récepteur aidera l'acteur en retour (Trivers, 1971). Trivers (1971) a proposé l'altruisme réciproque avec le maintenant célèbre dilemme du prisonnier qui décrit les stratégies alternatives (coopérer ou ne pas coopérer) entre deux joueurs. Dans ce dilemme, les gains sont distribués de sorte que le maximum de gain possible vient de la coopération conjointe. Cependant, le pire scénario pour un coopérateur est quand l'autre n'aide pas. Le dilemme émerge, car chaque joueur ignore la stratégie de l'autre. Dans la nature, la réciprocité est facilitée par des interactions répétées (Dridi et Akçay, 2018), par la familiarité (Keller et Reeve, 1998) et dans les populations structurées en groupe (van Veelan *et al.*, 2012). Un exemple de réciprocité abondamment cité est le partage de sang chez les chauves-souris vampires (*Desmodus rotundus*) (Wilkinson, 1984).

D'autres formes de réciprocité ont aussi été proposées et étudiées. La réciprocité indirecte repose sur la réputation, de sorte que les individus ont tendance à aider plus fréquemment les individus notoirement altruistes (Nowak et Sigmund, 1998). La réciprocité généralisée peut être résumée par l'action de payer au suivant; contrairement à la réciprocité directe, le receveur ne discrimine pas qui il aide en retour (Pfeiffer *et al.*, 2005). Enfin, la pseudo-réciprocité ne demande pas de réciprocité volontaire. L'acteur aide un receveur dont les actions égoïstes génèrent des bénéfices indirects à l'acteur (Connor, 1986).

La sélection de groupe, ou sélection multiniveau, est une hypothèse qui avance que la sélection peut s'appliquer à d'autres niveaux que l'individu. Ainsi, des groupes avec une fréquence d'altruisme plus élevée sont avantagés par rapport aux autres groupes (Maynard Smith, 1976). Donc, le comportement altruiste est promu lorsque les groupes altruistes ont un succès reproducteur meilleur que les groupes moins altruistes. La sélection de groupe peut s'appliquer à une variété de comportements dans différents taxons, mais les observations en nature restent rares (Goodnight et Stevens, 1997). La sélection de groupe a une histoire controversée en science, car une première proposition supposait que des animaux allaient moduler leur comportement pour le bien de la population (West *et al.*, 2007). Une grande quantité d'évidence empirique et théorique a réfuté cette première proposition et l'hypothèse de la sélection multiniveau, comme on la connait aujourd'hui, a pris son essor.

D'autres hypothèses existent, mais sont moins couvertes par la littérature. Par exemple, l'hypothèse de l'augmentation du groupe, discutée plus bas, est souvent invoquée en dernier recours, quand les autres hypothèses échouent à expliquer une situation de coopération (Wright, 2007). De plus, plusieurs hypothèses sont couramment impliquées dans la sélection d'un comportement altruiste. Des mérions couronnés (*Malurus coronatus*) subordonnés s'occupent de juvéniles avec lesquels ils sont apparentés, mais aussi des juvéniles non-apparentés; suggérant l'action conjointe des hypothèses de la sélection de parentèle et de l'augmentation de groupe (Kingma *et al.*, 2011).

La clé de l'étude de l'altruisme réside dans les coûts et les bénéfices du comportement. Par exemple, l'amplitude des coûts permet de qualifier un comportement d'altruisme fort (strong altruism) ou faible (weak altruism) (West *et al.*, 2007). Un comportement altruiste fort va diminuer l'aptitude phénotypique nette de l'acteur (Fletcher et Zwick, 2004 ; Trivers, 1971), tandis qu'un comportement altruiste faible peut augmenter l'aptitude phénotypique nette de l'acteur, mais sa valeur relative reste plus faible que celle du récepteur (West *et al.*, 2007). Le terme coopération, quant à lui, est souvent utilisé pour décrire un comportement qui produit un bénéfice pour autrui et qui est sélectionné grâce à ce bénéfice au receveur; le coût net sur l'acteur étant accessoire (West *et al.*, 2007).

La théorie des jeux est devenue experte à prédire la persistance de l'altruisme selon la distribution des coûts et des bénéfices. Pour ce faire, les modélisateurs vont définir des jeux pour décrire les interactions de coopération comme le dilemme du prisonnier, mentionné plus haut, ou le dilemme du volontaire (Diekmann, 1985). Le dilemme du volontaire est une instance du jeu de biens publics qui demande à un groupe de joueurs de choisir de contribuer à un ensemble de ressources qui sera redistribué entre l'ensemble des joueurs (Archetti et Scheuring, 2012). Spécifiquement, le dilemme du volontaire requiert à un seul joueur (volontaire) de payer un coût pour générer un bénéfice commun pour tous (Diekmann, 1985). D'autres dilemmes de la théorie des jeux incluent le jeu « snowdrift » (Kummerli *et al.*, 2007) et le dilemme du soldat (Clutton-Brock, 2009). La théorie des jeux traite aussi des stratégies optimales selon les conditions et de leur stabilité dans le temps (Maynard Smith, 1982). Par exemple, la stratégie tit-for-tat (faire ce que l'autre a fait au dilemme précédent) est proposée comme la stratégie optimale pour la réciprocité entre deux joueurs et est observée chez les épinoches à trois épines (*Gasterosteus aculeatus*) (Milinski, 1987).

Par définition, les comportements altruistes sont nécessairement sociaux, donc l'organisation sociale, c'est-à-dire qui interagit avec qui, devient capitale pour la sélection de l'altruisme. En fait, la plupart des mécanismes évolutifs de l'altruisme reposent sur l'organisation sociale (Nowak, 2006). Par exemple, une organisation en famille facilite la sélection de la parentèle (Eberhard, 1975). Une population organisée en groupe favorise les interactions répétées et donc la réciprocité directe (Van Veelan *et al.*, 2012). Différents groupes peuvent aussi présenter des disparités dans leurs aptitudes phénotypiques, permettant à la sélection d'agir entre les groupes (Maynard Smith, 1976). Les relations sociales sont même suggérées comme le moteur le plus important pour la persistance de l'altruisme, dépassant potentiellement la motivation et la cognition (Dale *et al.*, 2020). Hamilton (1975) avançait même que la sélection de l'altruisme était impossible sans appariement positif entre coopérateurs, c'est-à-dire sans un mécanisme permettant aux coopérateurs d'interagir entre eux. Ainsi, les bénéfices sont dirigés entre eux et non perdus aléatoirement dans la population.

La taille du groupe est aussi un déterminant important : la réciprocité dans le dilemme du prisonnier est généralement plus fréquente dans les petits groupes (Hamburger *et al.*, 1975), mais l'altruisme peut persister plus facilement dans les groupes plus larges pour les jeux de biens publics (Szolnoki et Perc, 2011). L'altruisme peut aussi influencer directement la taille des groupes, notamment dans les comportements altruistes reliés à la reproduction (Kokko *et al.*, 2001) et à la prédation (Krams *et al.*, 2010)

La présente thèse s'intéresse directement à la dynamique de coopération au sein des petits groupes temporaires; c'est-à-dire quelques individus non-apparentés seulement. L'objectif est de fournir des évidences et des explications sur les conditions qui favorisent la sélection de l'altruisme dans les petits groupes temporaires. La littérature sur le sujet est limitée, car les mécanismes permettant aux bénéfices de revenir vers l'acteur sont restreints. Des exemples de coopération entre petits groupes temporaires incluent les Grands Dauphins (*Tursiops truncatus*) qui s'associent en petits groupes pour la chasse (Daura-Jorge *et al.*, 2012) et les cichlidés (*Neolamprologus pulcher*) qui forment des groupes de dominants et de subordonnés en période de reproduction (García-Ruiz et Taborsky, 2022). La réciprocité généralisée a même été mesurée dans une expérience chez les humains (Fowler et Christakis, 2010). Les participants, organisés en une séquence de petits groupes temporaires et aléatoires, devaient choisir combien de ressources à partager au bien commun du groupe et l'altruisme, via une mécanique de réciprocité généralisée (payer au suivant), cascadait d'un groupe à l'autre (Fowler et Christakis, 2010).

Outre les enjeux de la vie en groupe (Krause et Ruxton, 2002), les petits groupes, en tant qu'organisation sociale, ont leur propre dynamique qui peut affecter la sélection de l'altruisme. Leurs membres deviennent rapidement familiers les uns avec les autres à la suite d'interactions répétées (Keller et Reeve, 1998). Les membres dans les petits groupes sont souvent plus coopératifs (Hamburger *et al.*, 1975), mais un groupe plus restreint peut être moins résilient à l'invasion de stratégies égoïstes que des groupes plus larges (Du, 2016). En elle-même, la taille du groupe est reliée à différents bénéfices (p. ex. division des tâches, dilution des risques de prédation, coordination) et lorsqu'un comportement altruiste augmente ou préserve la taille du groupe, les bénéfices générés sont accessibles à l'ensemble du groupe (Kingma *et al.*, 2014). Ce mécanisme évolutif est appelé l'hypothèse de l'augmentation de groupes (Kokko *et al.*, 2001). La stabilité des groupes est aussi un facteur important pour la sélection naturelle de tels comportements. Des groupes éphémères, comme dans les dynamiques populationnelles de fission-fusion (Couzin et Laidre, 2009), introduisent beaucoup de variations dans les interactions et donc dans les comportements (Bergmüller *et al.*, 2010). Cette variation qui émerge de l'environnement social s'ajoute à la variation qui existe déjà entre les individus (Barta, 2016) et pour un même individu au fil du temps et des différentes expériences (plasticité; Moran et al. 2022). Les variations interindividuelles et intra-individuelles sont souvent dirigées par la variation dans l'environnement social (McNamara et Leimar, 2010).

Étudier des comportements sociaux, comme l'altruisme, dans la nature, requiert des investissements considérables en temps et en ressources (MacColl and Hatchwell 2004). Les coûts et bénéfices ont souvent des conséquences sur le long terme comme la survie ou la reproduction de multiples individus ou groupes. De plus, manquer des individus ou des interactions est facile en nature, donc les données d'interactions sociales sont à risque d'être incomplètes (James *et al.*, 2009). Aussi, la coopération inclut généralement plusieurs processus simultanés, donc une grande quantité de données sont nécessaires pour départager les effets et les mécanismes en jeu. Pour pallier ces défis, j'ai donc utilisé une approche alternative pour étudier l'altruisme dans les petits groupes : un jeu vidéo comme système de recherche.

Les jeux vidéo ont beaucoup évolué dans les dernières décennies et deviennent de plus en plus complexes. Plus spécifiquement, les jeux massivement multi-joueurs (p. ex.: *Fortnite*, *World of Warcraft*, *Eve Online*) rassemblent simultanément des millions de joueurs dans des écosystèmes en ligne. Les concepteurs de ces jeux définissent une série de règles qui régissent les interactions des joueurs avec les éléments du jeu, mais aussi les interactions entre les joueurs. Ainsi donc, ces jeux en ligne se rapprochent d'écosystème naturel où les individus, ici les joueurs, interagissent avec des composantes abiotiques (p. ex.: le paysage, les ressources, les conditions changeantes) et avec des composantes biotiques (c'est-à-dire les autres joueurs). Les joueurs, étant des êtres pensants, prennent leurs propres décisions et sont souvent imprévisibles. L'ensemble des décisions des joueurs génèrent des propriétés émergentes dans la communauté et dictent souvent le sort du jeu en tant que produit. Notamment, les interactions entre les joueurs s'apparentent souvent à ce qu'on observe en nature : les joueurs sont en compétition entre eux pour des ressources ou des territoires, les joueurs peuvent s'entraider (altruisme), et enfin, ils peuvent se prédater en s'éliminant les uns les autres. Par exemple, les joueurs peuvent manifester des stratégies alternatives pour acquérir des ressources telles que la tactique du producteur ou du chapardeur (Vickery *et al.*, 1991), notamment dans le jeu *EVE Online*. Le temps de jeu étant limité, les joueurs font face à des compromis dans leur allocation de temps et d'énergie pour optimiser leur performance, similairement à ce qu'on peut voir en nature. Les joueurs vont régulièrement identifier et sélectionner les comportements les plus performants par rapport aux objectifs du jeu, modifiant ainsi la fréquence de différentes stratégies.

En réponse à la complexité et l'imprévisibilité des communautés de joueurs, les développeurs ont commencé à surveiller étroitement ce qui se passe dans leurs jeux. Pour ce faire, ils enregistrent ce que font les joueurs (leurs déplacements, leurs interactions, leurs décisions) sous la forme de base de données. Ces immenses bases de données sont une mine d'or pour les chercheurs de toute discipline. Outre les recherches abondantes sur l'utilisation directe des jeux vidéo, une nouvelle littérature profitant de données de jeux vidéo prend son essor. Par exemple, des épidémiologistes se sont intéressés à la propagation d'une vague de contamination dans World Of Warcraft en 2005 (Balicer, 2007 ; Boman et Johansson, 2007), car les similitudes avec une pandémie réelle étaient évidentes. Des sociologues investiguent l'impact du leadership et de l'identité de groupe dans l'émergence et le maintien de groupes organisés dans *Eve Online* (Milik, 2017). Beaucoup de sociologues explorent la nature des communications et des interactions entre joueurs, notamment au niveau de la toxicité (Aguerri *et al.*, 2023 ; Neto *et al.*, 2017 ; Wartna, 2023). Des écologistes s'intéressent aux stratégies de prédation (Fraser Franco *et al.*, 2022) et à la sélection sociale (Santostefano *et al.*, 2024).

Utiliser les jeux vidéo pour tester des hypothèses en biologie est une approche qui s'inscrit entre l'observation en nature, l'expérience contrôlée et la modélisation stochastique. Les écosystèmes virtuels se rapprochent de la complexité de la nature, mais tout peut être mesuré facilement, et parfois même contrôlé à l'instar d'une expérience. Comme la modélisation, les jeux vidéo peuvent aussi être considérés comme des versions simplifiées de la réalité, mais ils ont l'avantage d'inclure une variation organique provenant de décisions prises par des êtres vivants (Montiglio *et al.*, 2025).

En 2015, j'ai bâti un partenariat avec la compagnie de jeux vidéo montréalaise *Behaviour Interactif* qui a publié le jeu multi-joueurs *Dead by Daylight* en 2016. *Behaviour Interactif* accepte de partager ses données avec l'Université du Québec à Montréal pour les besoins de la recherche en écologie comportementale. En retour, les concepteurs de *Dead by Daylight* ont bénéficié des observations et des résultats de mes recherches pour mieux comprendre les comportements de leurs joueurs et améliorer le système pour une expérience plus engageante. *Dead by Daylight* est un jeu d'horreur multi-joueurs qui s'aligne très bien avec nos hypothèses. Dans ce jeu, un joueur incarne un prédateur tandis que quatre autres joueurs prennent le rôle des proies. Le but des proies est d'échapper au prédateur et de survivre, tandis que le but du prédateur est de traquer et capturer les proies. Le jeu se déroule dans différents environnements semi-ouverts où les proies doivent chercher et collectivement réparer cinq des huit génératrices dispersées dans l'espace pour pouvoir ouvrir les deux sorties possibles. Ces génératrices ont le rôle de parcelle de ressources à exploiter. De son côté, le prédateur peut blesser les proies et les capturer. Une fois capturée, une proie est immobilisée sur l'équivalent d'un « prey handling site ». Elle sera éliminée après trois minutes si personne ne vient la libérer. Ainsi, les proies peuvent manifester de l'altruisme en libérant les autres proies capturées pour leur éviter l'élimination (l'équivalent de la mort). Secourir une autre proie génère différents bénéfices, principalement pour la proie libérée, mais le sauveur s'expose à des risques plus élevés de prédation.

Les comportements exprimés par les proies dans *Dead by Daylight* ont maintes équivalences en nature. Les ongulés changent leur comportement d'approvisionnement (en groupe ou seul) en réponse à la prédation (Kie, 1999). Les proies restent vigilantes à la présence et aux déplacements du prédateur lorsqu'elles cherchent et acquièrent des ressources (Brown, 1999a ; Carey et Moore, 1986a ; Childress et Lung, 2003). Des corbeaux partagent des parcelles de ressources (Heinrich et Marzluff, 2016). Similairement aux proies dans *Dead by Daylight,* les insectes eusociaux mettent leurs ressources acquises en commun (Nowak *et al.*, 2010). Les proies évitent le prédateur de la même manière que dans la nature. Comme des cichlidés dans des refuges et des abris (Bergmüller *et al.*, 2005), les proies dans *Dead by Daylight* se cachent pour éviter d'être détectées par le prédateur. Au besoin, les proies fuient, possiblement en estimant la distance de fuite optimale (Altmann, 1958).

L'altruisme dans notre système d'étude est un comportement anti-prédation, donc un comportement dangereux face à un prédateur qui peut sauver la vie d'un congénère. Similairement, des suricates vont se regrouper pour houspiller les prédateurs (Graw et Manser, 2007). Aussi, des petits groupes de guppys (*Poecilia reticulata*) et des menées (*Phoxinus phoxinus*) vont inspecter des prédateurs approchant pour évaluer le niveau de danger et ensuite partager l'information à leur plus grand groupe (Pitcher *et al.*, 1986 ; Thomas *et al.*, 2008). Dans la nature, on retrouve même des mâles qui vont volontairement diminuer leur probabilité de survie pour protéger « leurs » femelles des prédateurs; par exemple, des mâles crickets (Gryllus campestris) vont laisser la femelle rejoindre le terrier en premier à l'approche d'un prédateur (Rodríguez-Muñoz *et al.*, 2011).

Le jeu vidéo *Dead by Daylight* nous permet donc d'avoir accès à une grande quantité de groupes bien définis composés d'étrangers et/ou d'amis. Le jeu nous permet aussi de mesurer des comportements altruistes qui incluent des risques et des bénéfices. Notre partenariat avec la compagnie *Behaviour Interactif* a permis aussi différentes approches scientifiques, incluant des observations du jeu tel quel, où nous avions accès aux données de millions de parties, et une expérience où nous pouvions fixer certains comportements pour tester nos hypothèses plus directement.

L'objectif central de cette thèse est d'identifier dans quelles conditions l'altruisme peut être sélectionné au sein des petits groupes temporaires. La présente thèse se veut une approche holistique qui explore chaque question sous différents angles. Le second chapitre de la présente thèse explore la composition des groupes (amis vs étrangers) pour investiguer comment la familiarité entre les membres d'un groupe impacte leurs comportements et leur survie. Dans la nature, la familiarité a différentes conséquences : les truites brunes (*Salmo trutta*) (Strodl et Schausberger, 2012) réagissent plus rapidement et acquièrent de la nourriture deux fois plus rapidement avec d'autres individus familiers qu'avec des individus non-familiers (Závorka *et al.*, 2015). La familiarité augmente la survie chez les mites (*Phytoseiulus persimilis*) (Strodl et Schausberger, 2012). Dans le jeu Dead by Daylight, le groupe de proies peut être composé d'étrangers, d'amis ou d'un mélange des deux. Les amis ont l'avantage de jouer régulièrement entre eux et de pouvoir communiquer; la coordination et l'échange d'informations sociales de qualité sont plus faciles qu'entre des joueurs étrangers ou non-familiers. J'émets l'hypothèse principale que la familiarité entre membres d'un groupe accélère la recherche de ressources, facilite la coopération et permet d'éviter les prédateurs plus efficacement. De plus, ces différents bénéfices s'additionnent à leur tour pour augmenter les probabilités de survie. L'approche statistique choisie, soit l'analyse de pistes, permet d'avoir une vue d'ensemble sur les différentes dynamiques en place dans le jeu. Donc, j'émets aussi l'hypothèse secondaire que les rencontres avec le prédateur créent un compromis d'allocation de temps envers d'autres tâches comme l'acquisition de ressources et l'altruisme. Ce second chapitre agit comme une introduction exhaustive à ce jeu vidéo comme système d'étude novateur.

Le troisième chapitre se concentre sur les coûts et bénéfices de l'altruisme pour identifier des mécanismes de sélection. Grâce à une expérience dans laquelle on fixe des phénotypes comportementaux altruistes et non-altruistes, je départage les différents coûts et bénéfices relatifs à l'altruisme. L'hypothèse centrale de ce chapitre est que l'altruisme, c'est-à-dire secourir les proies capturées, préserve la taille du groupe et donc permet aux proies de bénéficier des avantages reliés à un groupe plus large. Ainsi donc, on approche l'altruisme par ses effets sur la taille du groupe. Selon l'hypothèse de l'augmentation des groupes (Kingma *et al.*, 2014 ; Kokko *et al.*, 2001), je mesure des bénéfices dits actifs (le comportement des membres additionnels – receveurs – bénéficie directement l'acteur) et des bénéfices dits passifs (la seule présence de membres additionnels augmente la taille du groupe et cela génère des avantages). J'émets aussi la prédiction que les bénéfices passifs (prédation réduite, l'acquisition de ressources accélérée et sauvetages facilités) auront un plus grand impact positif sur la survie que les bénéfices actifs (réciprocité et ressources additionnelles). Les phénotypes purs permettent aussi de mener une analyse contextuelle qui inclut le niveau individuel (phénotype individuel) et le niveau du groupe (fréquence de phénotype altruiste) pour isoler les effets multiniveaux. Cette analyse permet de comparer simultanément différents mécanismes évolutifs susceptibles d'entretenir l'altruisme.

Les phénotypes purs du troisième chapitre ne permettent pas d'explorer pourquoi ou dans quelles circonstances les proies décident d'être altruistes. Donc, un quatrième chapitre explore la variation dans les comportements altruistes observée dans notre système d'étude. Je tente d'expliquer la variation intra- et interindividuelle, notamment due à la plasticité et à l'environnement social, pour identifier les mécanismes de sélection en jeu. En premier lieu, j'émets l'hypothèse qu'il y aura des joueurs systématiquement plus altruistes que d'autres, sachant que la littérature estime qu'en moyenne 35% de la variation comportementale émerge de différences entre les individus, c.-à-d. la répétabilité (Bell *et al.*, 2009). Ces différences peuvent être des différences de personnalité (Réale et Dingemanse, 2005) ou une variation systématique dans l'environnement social des individus. Deuxièmement, je teste l'hypothèse de la réciprocité généralisée : les proies seraient plus altruistes dans des groupes plus aidant ou venant de groupes plus coopérateurs, car elles « payent au suivant » (Pfeiffer *et al.*, 2005). Enfin, ma troisième hypothèse stipule que l'altruisme est influencé par l'expérience récente. Les proies auront plus tendance à aider si elles ont aidé et survécu dans leur partie précédente et si leur groupe était altruiste comme elles dans leur partie précédente. Les deuxième et troisième hypothèses visent à expliquer la variation intra-individuelle. La comparaison des modèles m'a permis d'estimer l'impact des hypothèses sur la variation de l'altruisme.

À la lumière de l’ensemble des résultats des trois articles, je pourrai ajouter des informations empiriques additionnelles à notre compréhension scientifique de la sélection de l’altruisme au sein de petits groupes temporaires et même aléatoires. Je démontre aussi la pertinence d’une approche holistique, car des comportements comme l’altruisme ou la familiarité ont plusieurs facettes et agissent simultanément sur différentes composantes des interactions entre individus. La présente thèse est aussi une base solide pour tous ceux qui voudraient utiliser les jeux vidéo comme système d’étude en biologie. J’y traite des différents avantages, mais aussi des limites de cette approche novatrice.

CHAPITRE 2

Indirect effect of familiarity on survival: a path analysis on video game data

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2.1 Mise en contexte

La familiarité est une composante émergeant d'une organisation sociale agrégée en groupe ou en réseau social dense. Elle est donc importante à adresser en premier lieu lorsqu'on s'intéresse aux comportements sociaux comme l'altruisme. Dans ce second chapitre, je veux comprendre comment la familiarité entre les membres d'un groupe impacte ultimement leur survie. La familiarité peut faciliter la communication et la coordination. Ainsi, les membres d'un groupe familier peuvent partager des informations comme la présence de ressources ou de prédateurs. Ils peuvent aussi coordonner leurs stratégies pour s'attaquer à des proies plus grosses ou moins accessibles. Nous posons donc l'hypothèse que la familiarité améliore la survie de façon indirecte en facilitant des comportements qui sont eux capitaux pour la survie (p. ex. : l'acquisition de ressources, la coopération, la prédation).

Dead by Daylight est tout indiqué pour tester ce genre d'hypothèse, car les joueurs qui contrôlent les proies peuvent être amis ou étrangers, créant ainsi des groupes plus ou moins familiers. Un joueur dans un groupe exclusivement composé de ses amis, bénéficie des informations et de la coordination avec trois autres membres de ce groupe. Ces bénéfices ne sont pas accessibles dans les groupes composés d'étrangers, et moindres dans des groupes mixtes.

2.2 ABSTRACT

Familiarity between members of the same group is predicted to play a role in many biological processes. Familiarity can facilitate recognition, aggregation, communication, coordination, and altruism between group members. We tested a path of interrelated hypotheses on the effect of familiarity on survival, resource acquisition, predator avoidance, and altruism. We predicted that individuals with familiar members in their group would have higher survival, acquire resources faster, avoid predators more easily, and perform more altruistic actions. We used data from an online video game (*Dead by Daylight*) where small groups of four players (i.e. prey) must exploit resource patches while avoiding a predator. Prey can help fellow prey when the predator catches them (altruism). Using a video game as a study system provided access to a large behavioural dataset that would otherwise be difficult to obtain in nature. Using path analysis, we found evidence that coordinated resource acquisition and helping behaviours increased with the number of familiar individuals in the group. However, more altruistic actions increased their encounters with the predator and thus reduced their survival. When accounting for all indirect effects of familiarity on survival (through resource acquisition, altruism, and predator-prey encounters), familiarity had a small indirect net positive effect on survival.

Keywords: familiarity, selection, predator-prey, cooperation, resource acquisition, survival, path analysis, video game

2.3 INTRODUCTION

Living in close proximity to, and interacting with, conspecifics provides fitness benefits (Alexander, 1974). For example, group-living reduces predation risk in large herds of elk (*Cervus elaphus*) and improves foraging success in wolves (*Canis lupus*) (Hebblewhite et Pletscher, 2002). Repeated social interactions among individuals that can recognize each other create a familiarity that persists over time (Bhat et Magurran, 2006 ; Gutmann *et al.*, 2015). Individuals interacting preferentially with familiar conspecifics can accrue benefits such as access to more social information, improved coordination of group maneuvers (Pitcher, 1986), increased predator detection (Griffiths *et al.*, 2004 ; Pays *et al.*, 2013), easier social learning, and reciprocity (Barber et Wright, 2001). Familiarity is thus likely to impact fitness (survival and reproduction) indirectly through its effects on predator avoidance, resource acquisition, and altruistic behaviours (Scheiner *et al.*, 2000 ; Ward et Hart, 2003). For example, wild juvenile brown trout (*Salmo trutta*) reacted 14% faster to predators and foraged twice as fast when they were with familiar conspecifics than when with unfamiliar ones (Griffiths *et al.*, 2004). Group-living *Phytoseiulus persimilis* mites reacted faster to predators and had higher survival rates when with familiar individuals (Strodl et Schausberger, 2012). Familiar individuals can build trust through repeated interactions and be more likely to perform costly behaviour that benefits familiar individuals (Keller et Reeve, 1998 ; Roberts et Sherratt, 1998). Small groups of familiar fathead minnows (*Pimephales promelas*) were more cohesive than unfamiliar ones (Chivers *et al.*, 1995). This allowed them to perform more anti-predatory behaviours like dashing and inspecting, suggesting that having familiar individuals in one's group increased the probability of surviving encounters with predators. Familiarity can also shape communication when individuals discriminate signals and are more attentive to familiar or local individuals. For example, Australian sea lions, *Neophoca cinerea*, are less responsive and less aggressive to barks from unfamiliar males than they are to calls from familiar males during mate guarding season (Attard *et al.*, 2010). Female guinea pigs, *Cavia aperea* f. *percellus*, respond more strongly to calls from familiar pups than from unfamiliar ones (Kober *et al.*, 2007). Flocks of familiar Carolina chickadees, *Poecile carolinensis*, had different note compositions in their calls than groups of unfamiliar individuals (Coppinger *et al.*, 2019).

Assessing the impact of familiarity on fitness through its effects on interrelated traits is extremely difficult. Observations on social interactions and familiarity in the wild are generally incomplete because important interactions or individuals can be missed (James *et al.*, 2009), and linking social interactions, behavioural traits, and fitness requires intensive monitoring. Video games offer a rare opportunity to assess the indirect effects of familiarity on fitness through predator avoidance, resource acquisition, and altruism. Many video games take place in a spatially structured virtual environment where players control avatars, the digital representation of themselves in the game. Often, multiple players can interact in the same virtual environment. For the players, the objective is often to survive each trial by adopting tactics that maximize survival. Hence, video games offer an environment where players can exhibit complex and ecologically realistic behaviours. They represent opportunities to gain insights on how the environment and the characteristics of social interactions generate selection on behavior.

We explored the effects of familiarity on survival in the multiplayer video game *Dead by Daylight* (*Behaviour Interactive*, Montreal, Canada). *Dead by Daylight* is a game that places one player in the role of the predator whose objective is to hunt and capture the other four players (henceforth referred to as prey). The prey must collectively acquire resources while avoiding the predator. Once prey obtain a certain quantity of resources, they can escape through one of the two exits. The predator must hunt, capture, and eliminate each prey before they exit. Prey can cooperate and rescue each other if they are captured by the predator. If a group of prey fails to gather enough resources to open an exit, an alternative exit is enabled for the last living prey. Prey in the same four-player group can be unfamiliar or familiar (i.e. choosing to play together) to each other. Our objective is to measure the indirect impacts of familiarity among prey on their survival via different fitness-related behaviours (solid lines in Figure 2.1).

Given that familiar players can recognize each other and can communicate and coordinate their behaviour in the game, our main hypothesis is that familiarity among prey will yield a positive total effect on survival. To address this hypothesis, we need to tackle three sub-hypotheses on the indirect paths through which familiarity affects survival.

First, we hypothesize that familiar prey will acquire resources faster because familiarity increases coordination, which should increase resource acquisition rate (Figure 2.1, path *a* + b), and acquiring resources is the key behaviour enabling players to exit the game and survive (Figure 2.1, path *c*). Encounters with the predator will negatively impact survival (Figure 2.1, path *g*). Our second sub-hypothesis states that prey with familiar individuals in their group will avoid the predator more easily (Figure 2.1, path *d*) due to potential communication and transmission of information about the predator spatial location among familiar individuals. Third, we hypothesize that familiar prey can mitigate the costs of altruism in terms of predation risk (Figure 2.1, path *i*) because they can share information about the predator. We predict that altruism (helping injured or captured prey) will impact the number of prey that are alive who can participate in acquiring the necessary resources for survival (Figure 2.1, path *k*) and who can help in return (reciprocity).

Additionally, time might trade-off with various behaviours expressed by prey. For example, being chased by the predator or helping others leaves less time to acquire resources (Figure 2.1, path *f* and *m*). Evading the predator also takes time from helping fellow prey (Figure 2.1, path *h*). We will quantify the relative importance of familiarity among prey on their survival (main hypothesis) by estimating the strength of the effect of resource acquisition (sub-hypothesis 1), predator-prey encounters (sub-hypothesis 2), and helping others (sub-hypothesis 3) on the likelihood of prey survival.

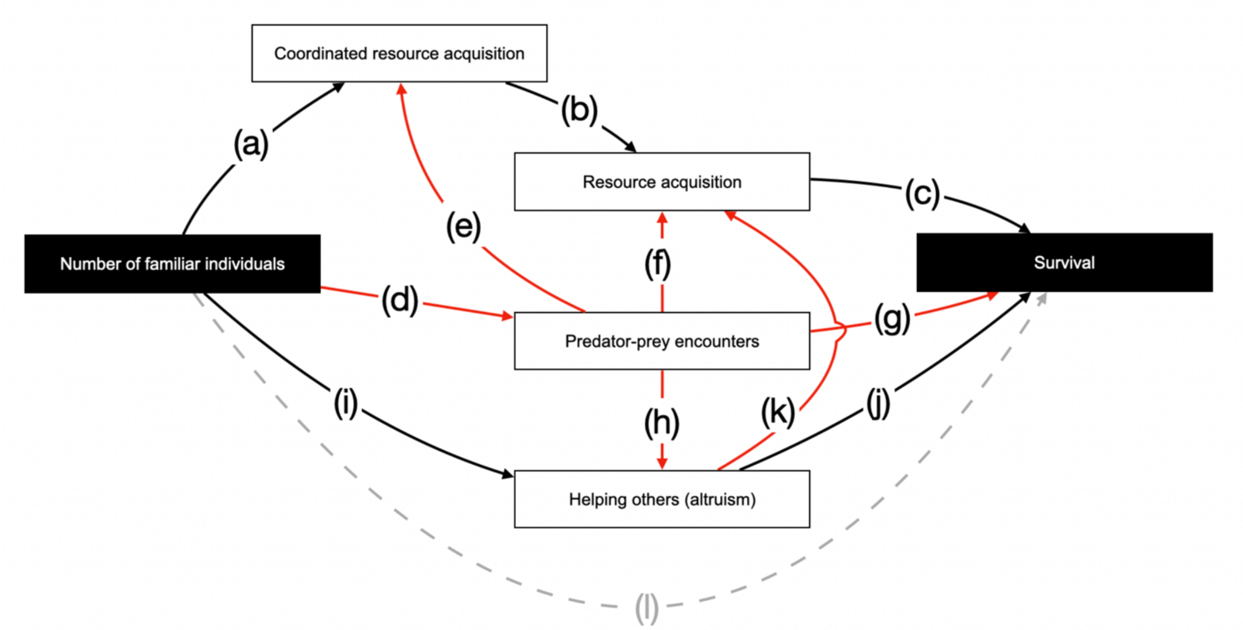

Figure 2.1 Predicted paths of behavioural traits of prey in our system according to our hypothesis. Solid lines represent the indirect effects of familiarity on survival through coordinated resource acquisition, predator avoidance, and helping others (altruism). Black paths represent positive effects and red paths are negative effects. The dashed line represents the residual effect of familiarity on survival.

2.4 METHODS

2.4.1 Study system

Each trial of *Dead by Daylight* begins when five players (four prey and a predator) are selected and grouped; trials end when every prey has either been eliminated or has escaped. Trials last, on average, 10 minutes but there is no time limit. By default, players (prey) in each trial are randomly assigned to a group with three other unfamiliar prey of similar skill. Prey can also actively pair themselves with one to three familiar individuals. Therefore, groups of prey can be composed of four unfamiliar, four familiar, or a mix of both familiar and unfamiliar individuals. Any focal prey can have between zero to three familiar individuals in their group. Trials in which the predator was familiar with any of the prey were removed. Prey have access to public information: at any given time, each prey knows the status of the other prey (healthy, injured or captured) as it is displayed on the interface of the game and it can easily locate the position of a captured prey. All prey can also see each other (and their respective behaviour) when in close proximity. However, the game offers no way for verbal or written communication between group members during a trial, but a survey conducted on the community of players of *Dead by Daylight* (independent of this study) reported that 97.5% of players use external software to communicate with familiar group members while playing (Céré, unpublished results). Although familiar prey likely share more social information than unfamiliar prey, we have no way to measure the quality or quantity of the information that is shared. Hence, in our study system, familiarity may encompass many mechanisms: familiar individuals use a strict form of vocal discrimination (Attard *et al.*, 2010), can recognize each other, and can more easily coordinate behaviours such as acquiring resources and altruism. Our data do not include whether familiar players are related or not.

Data are recorded by the system and stored on an online server. We used data from a five-week period (14 September – 17 October) in 2018. Data include measures of behaviour, performance and social connections between prey. Prey receive points for their behaviour in the trials (acquiring resources, predator-avoidance, altruism). At the end of every trial, encounters with the predator are counted and continuous values represent the quantity of resources acquired and number of helping actions (ranging from 0 to 8000).

Before each trial, the game system generates a unique virtual environment offering cover in the form of trees, rocks, walls, and hills. The resource patches that the prey must find and exploit, as well as the prey-handling site where the predator takes its captured prey, are uniformly distributed in the environment.

Figure 2.2 (a) view of the environment, (b) the predator in front of a prey handling site (hook), (c) a prey exploiting a resource patch (generator) and (d) prey hiding to avoid the predator.

2.4.2 Behaviours of prey

In our system, prey behaviour comprises acquiring resources, predator evasion, and a suite of altruistic behaviours. First, prey must search for and exploit resource patches. The main goal of the prey in this video game is to collectively exploit five out of the eight resource patches in the environment. Thus, searching for resources is the default behaviour, meaning that it is the behaviour that prey perform when no other external pressure is placed on it (i.e. flee the predator or rescue a fellow prey). It is possible for prey to spend the entire trial acquiring resources.

2.4.3 Resource acquisition (sub-hypothesis 1)

Prey are awarded points for time spent actively exploiting patches; the ability of any prey for resource acquisition (variable: *resource acquisition*) is automatically recorded. Multiple prey can exploit the same patch at the same time to exploit a patch faster. Prey are also awarded points for any second spent on coordinated resource acquisition with other prey (variable: *coordinated resource acquisition)*. Once five out of the eight resource patches of the trial have been fully exploited, two exits open and prey can escape the trial (and survive). When there is only one prey remaining, a hidden escape route appears randomly in the environment: if the prey finds it, it can escape and survive even though the five resource patches have not been fully exploited.

2.4.4 Predator-prey encounters (sub-hypothesis 2)

In addition to acquiring resources, prey can also avoid the predator. Vigilance, fleeing or hiding are behaviours that are assumed to trade-off with acquiring resources (Brown, 1999). Any action by the prey (fleeing, exploiting the patches, helping others) creates noise that can attract the predator. The predator can also look for tracks or signs of prey presence. A prey hears an audio signal whenever the predator is close to their position as personal information. When the predator encounters a prey, it pursues it as it can run faster than prey. The number of pursuits (variable: *predator-prey encounters*) a prey is involved in during a trial is our proxy for predator avoidance; the lower the number, the greater the predator avoidance. The prey can be injured by the predator, thus forcing it to make noise and leaving tracks. A prey can also be captured by the predator and taken to a prey-handling site. The prey is then immobilized, and a countdown starts whereby the prey is eliminated from the trial after 180 seconds.

2.4.5 Helping others (sub-hypothesis 3)

In addition to acquiring resources and anti-predator behaviour, prey can also heal an injured prey or free a captured prey. Thus, opportunities for helping others arise after prey fail to evade the predator. In the wild, similar reactive and altruistic behaviours include alarm calling (Sherman, 1977) and mobbing (Graw et Manser, 2007). Opportunities for helping other are publicly advertise as captured prey are highlighted and thus easily found from anywhere in the trial. In addition, the health state of each prey is always shown on the interface of the game, although injured prey are not highlighted as captured prey are. Helping other prey can be time consuming, thus reducing time dedicated to acquiring resources. Individuals are awarded points for any successful helping actions (variable: *helping others*).

A more detailed description of the game can be found in Appendix A.

2.4.6 Data sample and analysis

Testing our hypotheses requires quantifying the relationships among multiple behavioural traits. We used path analysis to assess the consequences of familiarity for fitness through its indirect effects on resource acquisition, predator-avoidance, and altruism (Shipley, 2016). We will compare our hypothetical path models with strictly indirect effects from familiarity on survival with a model that also includes a direct path (Figure 2.1, path *n*). This will allow us to test if there are residual effects of familiarity on survival that are not accounted for by our hypothesized indirect paths, such as aggregation or receiving more help through reciprocity.

Briefly, path analysis constructs a covariance matrix based on a hypothetical series of relationships (path in Figure 2.1) and compares it to a covariance matrix produced from the observed data. The model of the path analysis minimizes the difference between the hypothetical and the observed matrix. Path analysis is widely used in animal behaviour and evolutionary biology studies (Kelly *et al.*, 2008 ; Santostefano *et al.*, 2017 ; Scheiner *et al.*, 2000 ; Sih *et al.*, 2002).

The duration of a trial impacts the number of actions that a prey can perform; longer trials offer more opportunities to acquire resources or to help other prey. Thus, we included the duration of the trial (in seconds) in the statistical model as a potential impact on helping others, predator-prey encounters, resource acquisition and coordinated resource acquisition. It was not included in the figure nor in the results for clarity (see Appendix B for the complete model).

We retained only players who played the game on a computer. We removed trials where either the predator or a prey disconnected before the end. Technical issues (trials ending prematurely or not ending properly due to a server malfunction) created inflated values in our dataset. We thus removed the lowest and highest 1% of values for each of our continuous variables, which accounted for 1.9% of our complete dataset; the total number of filtered data points was less than the expected 2% due to some observations being filtered out for multiple inflated values. This approach removed trials shorter than 95 seconds and longer than 1260 seconds and removed trials with more than nine encounters between a prey and the predator. More than nine encounters suggested the possibility of the prey and the predator cheating together and deliberately encountering each other to gain more points. Retaining the extreme observations (1.9% of the dataset) produced the same qualitative result but we preferred excluding them to ensure that our results were robust and reproducible. We also excluded each player's first 10 trials to ensure that our observations were from players with a basic knowledge of the game; 10 is a conservative number of trials for a player to grasp the objectives of the game. We assumed that players would increase their time spent acquiring resources and the frequency of altruistic behaviours while decreasing the number of their encounters with the predators with each additional trial played. Hence, we included in the model the number of trials completed by the players prior to each trial as a covariate. For clarity, we did not present the number of previous trials in the figures nor in the results (see Appendix B for the complete model). We kept a single randomly selected prey per trial and one randomly selected trial per prey to avoid pseudoreplication.

Path analysis assumes that all variables follow a multivariate normal distribution and that there is no feedback loop in the causal relationships (directed graph). No relationship in our hypothesized model involved a feedback loop such as A favours B and the increase of B favours A. Our sample size (n= 11 282 trials) ensured that our results were not biased by any departure from multivariate normality, as would any dataset smaller than 1000 observations (Shipley, 2016). We also ensured that the relationships that we estimated in our path analyses did not include an important non-linear component (see Appendix C).

We conducted path analyses using the package *lavaan* (Rosseel, 2012) in the statistical environment R v3.5.1 (R Core Team, 2020). We tested the fit of our model by using the Comparative fit index (CFI), the Tucker-Lewis index (TLI), and the Root mean square error of approximation (RMSEA); values of >0.95, >0.95 and <0.05, respectively, indicate a good fit (Hooper *et al.*, 2008). A good fit suggests that the observed and hypothesized covariance matrices are not different, and that the data thus support our predicted paths. We re-ran our model after removing the relationships that were not statistically significant ($p>0.05$) until we reached the best fit. We used standardized partial regression coefficients to estimate the direct effect of familiarity, and its indirect effects through resource acquisition, predator avoidance, and helping others (altruism).

A path between two variables depends on the direction of the relationship. The single path coefficient between two connected variables is the direct effect. Along with the direct effect, two variables can be linked via other variables, for example the number of familiar individuals indirectly impacts helping others through its direct impact on predation (Figure 2.1, path *d*), which itself impacts helping others (Figure 2.1, path *h*). Multiplying the path coefficients on the same path (a series of directed relationships) gives the indirect effect of an exogenous variable (independent variable with no path pointing at it) on the endogenous variable (dependant variable). Summing the direct and indirect effects gives the total relationship between two connected variables.

We used the size of the total effect between our behavioural traits to test our predictions that the number of familiar prey increases individual survival probability by increasing resource acquisition, helping others and reducing predator-prey encounters. We then dissected the direct and indirect effects between the interrelated behavioural traits (resource acquisition, coordinated resource acquisition, predator avoidance, helping others) to explore their opposing and synergetic effects on survival.

Following the results of our path analysis (see below), we perform an additional analysis to facilitate our interpretations of whether helping others accrued benefits through reciprocity. We analyzed the probability of a given player being rescued from the prey handling site as a function of their average rate of helping others (*helping others* score divided by time) using a random sample of 10,000 trials collected on 14 September 2018 and a generalized linear model (GLM) with binomial error distribution (not included in the path analysis).

Means are given ± 1 standard deviation (unless otherwise noted) and all statistical tests are two-tailed (α=0.05).

2.5 RESULTS

From 11,330 available prey in 41,763 trials, we kept one randomly selected player per trial and one trial per player, resulting in a final dataset of 11,282 unique observations (trials and prey) for our path analysis. Focal prey could have zero (n=7159), one (n=1 2525), two (n=1111), or three (n=485) familiar individuals in their groups. The overall survival probability was 37.4% (3671 survived). On average, prey encountered the predator 3.40±2.24 times per trial (range=0-9). Prey received an average of 3205±2127 points for acquiring resources (range = 0-8000), an average of 484±553 points for coordinating resource acquisition (range=0-3874), and an average of 1307±1467 points for helping others (range=0-8000).

2.5.1 Model fit and main hypothesis

Our full model (Figure 2.3) did not have a good fit (Table 2.1, model 1) because the direct effect from familiarity on survival (path n) was not significant. The model in which familiarity only had indirect effects on survival (Figure 2.3) achieved the best fit (Table 2.1, model 2). We predicted that predator encounters would reduce opportunities to help others for the focal prey since predator evasion consumes time. Contrary to this prediction, however, helping others increased with predator-prey encounters (path *h* was positive). It is unlikely that encountering the predator increases altruism. Rather, by switching the direction of the path, we obtain a relationship that is more intuitive: helping others increases your probabilities of encountering the predator. The model with that modification (changing the causal direction to helping others positively impacting predator-prey encounters; model 2’ in Table 2.1) gives an equally good fit to the accepted model (model 2 in Table 2.1). The correlation matrix can be found in Table 2.2. The overall indirect effect is the result of the sum of all the path coefficients from the number of familiar individuals to survival in our model (i.e. combining paths *a* to *k* in Figure 2). Overall, the number of familiar individuals in a group indirectly increased prey survival, but this total effect was small (Figure 2.4, total effect = 0.013 ± 0.005, Z= 2.42, p<0.001).

Table 2.1 Fit of the path models based on our hypothesis. Bold values indicate a good fit according to the Comparative Fit Index (CFI), Tucker–Lewis index (TLI), and Root Mean Squared Error of Approximation (RMSEA).

	Number of parameters	CFI	TLI	RMSEA
(1) Full model with direct (path n) and indirect effects	**9**	**0.979**	**0.958**	0.052
(2) Model with strictly indirect effects	**8**	**0.978**	**0.964**	**0.049**
(2') Model with strictly indirect effects – helping others positively impacting predator-prey encounters	**8**	**0.980**	**0.967**	**0.046**

Table 2.2 Correlation matrix of the behavioural traits of the alternative path model.

Observed Variables	Number of familiar individuals	Predator-prey encounter	Helping others (altruism)	Coordinated resource acquisition	Resource acquisition	Escaped
1. Number of familiar individuals	-	-	-	-	-	-
2. Predator-prey encounter	0.119	-	-	-	-	-
3. Helping others (altruism)	0.099	0.345	-	-	-	-
4. Coordinated resource acquisition	0.067	0.056	0.113	-	-	-
5. Resource acquisition	0.054	0.066	0.152	0.808	-	-
6. Escaped	-0.000	-0.054	0.018	0.329	0.522	-

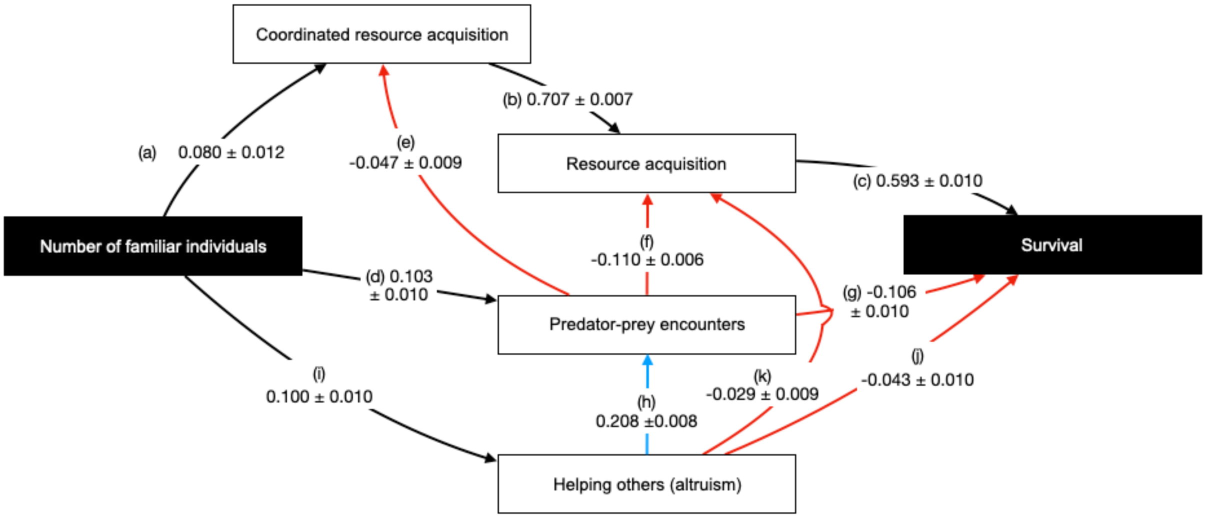

Figure 2.3 Path coefficients of the indirect effects of familiarity on survival. Black and red paths signify positive and negative relationship respectively. The blue path *(h')* is a positive because the direction changed from negative in the hypothetical model to positive. All shown paths are significant relationships (p<0.001).

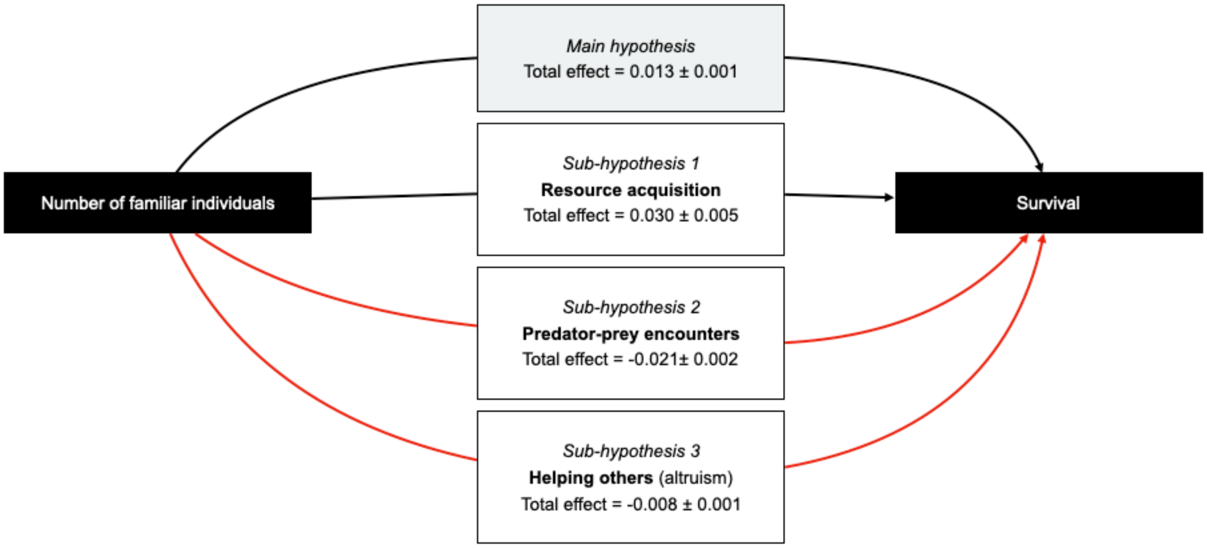

Figure 2.4 Total indirect effect of the number of familiar individuals in a group on survival (main hypothesis; grey box) and via different indirect paths: resource acquisition, predator-prey encounters and helping others (altruism).

2.5.2 Resource acquisition (Sub-hypothesis 1)

The number of familiar individuals in a group increased coordinated resource acquisition (Figure 2.3, path *a*: estimate= 0.080 ± 0.012, Z=6.820, p<0.001), which in turn, increased overall resource acquisition (Figure1.3, path *b*: estimate=0.707 ± 0.007, Z=107.280, p<0.001). Helping others (Figure 2.3, path *k*: estimate=-0.029 ± 0. 009, Z= -3.327, p=0.001) and predator-prey encounters (Figure 2.3, path *f*: estimate= -0.110 ± 0.006, Z= -19.29, p<0.001) decreased resource acquisition. Hence, the number of familiar individuals only had an indirect effect on resource acquisition (Figure 2.3: estimate= 0.051 ± 0.008, Z= 6.153, p<0.001) through coordinated resource acquisition. Acquiring resources favoured survival (Figure 2.3, path *c*: estimate= 0.593 ± 0.010, Z= 60.33, p<0.001). Resource acquisition was the strongest positive indirect path from the number of familiar individuals on prey survival (Figure 2.4, total effect = 0.030 ± 0.005, Z= 6.13, p<0.001).

2.5.3 Predator-prey encounters (Sub-hypothesis 2)

Prey that were grouped with more familiar individuals encountered the predator more often (Figure 2.3, path *d*: estimate= 0.103 ± 0.010, Z= 10.17, p<0.001). More frequent predator encounters had a negative impact on resource acquisition as expected (Figure 2.3, path *f*: estimate= -0.110 ± 0.006, Z= -19.29, p<0.001). Encountering the predator more often was associated with a lower level of coordinated resource acquisition (Figure 2.3, path *e*: estimate= -0.047 ± 0.009, Z= -5.02, p<0.001) and lower survival probability (Figure 2.3, path *g*: estimate= -0.106 ± 0.010, Z= -10.97, p<0.001) through an increased probability of capture. The total indirect effect of familiarity on survival via predator-prey encounters was weak but negative (Figure 2.4, total effect = -0.021 ± 0.002, Z= -9.67, p<0.001).

2.5.4 Helping others (Sub-hypothesis 3)

Familiar prey successfully help others more frequently (Figure 2.3, path *i*: estimate= 0.100 ± 0.010, Z= 10.33, p<0.001). Prey that help other more frequently acquired fewer resources (Figure 2.3, path *k*: estimate= -0.029 ± 0.009, Z= -3.33, p<0.001). Helping others directly increased the number of encounters with the predator (Figure 2.3, path *h’*: estimate= 0.208 ± 0.008, Z= 25.89, p<0.001) and decreased the probability of survival (Figure 2.3, path *k*: estimate = -0.043 ± 0.010, Z= -4.09, p<0.001). Overall, familiarity had a weak but negative indirect effect on survival via helping others (Figure 2.4, total effect = -0.008 ± 0.001, Z= -6.22, p<0.001).

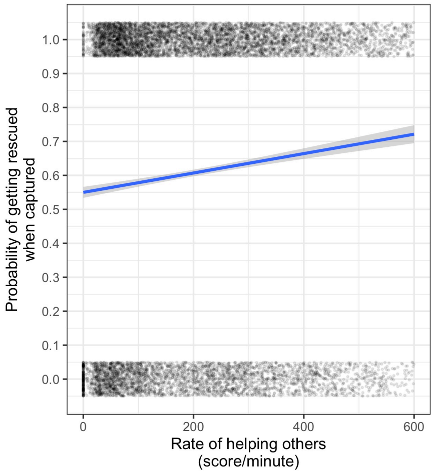

Figure 2.5 Impact of helping others on the probability of being rescued when captured. The slope is the result of a generalized linear model with a binomial distribution and the points are jittered for visibility.

Helping others more frequently increases a prey's probability of rescue by a fellow prey when captured within the same trial (GLM, estimate= 0.1290 ± 0.0210, Z= 6.125, p<0.001): the probability of being rescued increased approximately by 15% from the most selfish to the most helpful prey (rate of helping others of 600 points per minutes) (see Figure 2.5).

2.6 DISCUSSION

We used an online multiplayer video game to test the hypothesis that being familiar with members of a group would indirectly increase one's survival by improving resource acquisition, predator avoidance, and altruism. We found that resource acquisition had a positive effect on survival with coordination in acquiring resources being an important component. In line with our first and third sub-hypotheses, an increased number of familiar individuals within groups increased the frequency of coordinated resource acquisition and altruism. This could be explained by familiar individuals communicating their spatial position to each other and therefore being able to coordinate their actions more easily while exploiting resource patches or helping others. However, this did not seem to help in avoiding the predator. Contrary to our second sub-hypothesis, having more familiar group members led a given prey to encounter the predator more often, which decreased survival. Nonetheless, familiarity among group members, which in our system facilitated communication, recognition and coordination between kin or non-kin individuals, slightly increased prey survival. Hence, traits that help develop and maintain familiarity with conspecifics could be favoured in the game, therefore supporting our main hypothesis. That we found no other significant residual effects (direct) than the hypothesized indirect effects, suggests that we captured the full effect of prey familiarity on survival in this system.

2.6.1 Resource acquisition (Sub-hypothesis 1)

We supported our sub-hypothesis stating that familiar prey coordinated resource acquisition better, suggesting a higher overall level of aggregation. Aggregation is suspected to be easier if familiar prey communicate their respective location or if they can predict the behaviour and location of others based on past experience. Testing this aggregation hypothesis would require monitoring the spatial location of individuals in our trials, which is beyond the scope of our study. Studies in natural settings support this hypothesis as familiar individuals tend to aggregate more (Jacoby *et al.*, 2012 ; Thorington et Weigl, 2011) and larger groups of prey are more readily detected by predators (Krause et Ruxton, 2002). For example, larger aggregations of caddisflies (*Rhyacophila vao*) (Wrona et Dixon, 1991) and elk (*Cervus elaphus*) (Hebblewhite et Pletscher, 2002) encounter predators more often and blue acara cichlids, *Aequidens pulcher*, prefer to hunt larger shoals of prey (Krause et Godin, 1995). The effect of familiarity on coordinated resource acquisition is responsible for the overall positive effect on survival.

2.6.2 Predator-prey encounters (Sub-hypothesis 2)

We predicted that prey in groups with more familiar partners would be better at avoiding the predator, especially if they exchanged valuable social information on the whereabouts of the predator. On the contrary, we observed an increase in predator-prey encounters for individuals with more familiar individuals in their group. A possible explanation is that familiar group members may share social information about the predator, but that information may overlap with what they already know from personal information (i.e. auditory cues when the predator is near), thus it does not bring any additional insight to help avoid the predator. Redundant information could explain the lack of predicted benefits of vocal communication in avoiding the predator but it cannot explain the additional increase in predator-prey encounters. In that regard, it is unlikely that communication alone increased predator-prey encounters. It is possible that prey might stay closer to familiar partners for coordinated resource acquisition or helping each other, thus increasing their detectability by the predator.

As predicted, we found that increased predator-prey encounters lowered the resources acquired. The costs of acquiring resources appear to be low in our study (prey can simultaneously acquire resources and detect predators) but there seems to be a time allocation trade-off between predator-evasion behaviours and resource acquisition as stated in our predictions. Such a time allocation trade-off is common in nature. For example, yellow-bellied marmots (*Marmota flaviventris*) spend 10% of their resource acquisition time on vigilance (Carey et Moore, 1986), Trinidadian guppies (*Poecilia reticulata*) trade off feeding with hiding (Fraser et Gilliam, 1987), and ungulates modify their foraging strategy (energy maximization) in the presence of predators (Kie, 1999).

2.6.3 Helping others (Sub-hypothesis 3)

The frequency of successfully helping others increased with the number of familiar individuals that one has in its group. Familiar prey were potentially better at helping others because they could communicate and coordinate a safe rescue when the predator was away. Also, familiar prey could have performed more attempts at helping others due to their being generally closer to prey in need. It is important to note that our data did not account for failed attempts at helping others such as attempts that are interrupted by the predator. Consequently, prey with familiar individuals in our study were either attempting to help more frequently or were better at performing help. However, in the model, failed (interrupted) attempts at helping might be mathematically accounted for in the direct path (Figure 2.1

path *d*: familiarity – predator-prey encounters) that would include such residual indirect effects otherwise not included in the model. We predicted that frequent predator encounters would lower the opportunity for helping others, but our results suggest the opposite: helping others significantly increased the number of predator-prey encounters. In our system, injured or captured prey attract the attention of the predator via auditory (e.g. loud noises) and visual (e.g. blood on the soil) cues. Thus, prey probably encountered the predator frequently while helping others. In summary, this suggests that familiar prey increased their encounters with the predator because they successfully help more (path *i-h'*: familiarity – helping others – predator-prey encounters) and failed more often when trying to help others (path *d*: familiarity – predator-prey encounters).

Contrary to our predictions, we found that helping others reduced survival. We predicted that rescuing or healing a fellow prey would preserve group size, which would thereby increase risk dilution, effort in acquiring resources, and the possibility of being rescued if captured (Nowak, 2006 ; West *et al.*, 2007). Indeed, our data suggest that prey might reciprocally helping others because helpful prey have a higher chance of being rescued when captured. Additionally, our data suggest that helping others, in conjunction with increased prey encounters, decreased the time allocated to acquire resources and thus reduced the likelihood of exit-opening. We proposed that one of the indirect benefits of helping others was to rescue a fellow prey who would then be able to assist in resource acquisition and thus increase the probability of escape. In contrast to this prediction, the alternative exit that the last remaining prey (if all the other prey are dead) can use to survive without reaching the resource threshold likely mitigates the benefit of rescuing others (and overall altruism) for the additional effort of resource acquisition. One possible survival strategy would be to wait for others to get eliminated in order to gain access to this alternative exit. Prey survived by using this escape route in 16% of our trials. By definition, altruistic actions are costly to the individual that performs them and beneficial to the recipient (West *et al.*, 2007) and can evolve when the indirect fitness benefits of helping others outweigh the fitness costs. In our system, we can conclude that increased predation risk and lower time allocation for resource acquisition experienced for helping others outweigh the benefits. Moreover, the fact that the direct path from helping others to survival is still negative, even after controlling for its indirect paths, suggests that there are other residual mechanisms that make helping others detrimental to survival. This negative impact of altruism is probably mitigated, but not cancelled, by benefits like reciprocity and preserved group size. It is possible that selection for such system of altruism could exist at the level of the group and such hypotheses would merit testing in the future. It would also be interesting to estimate the payoffs of helping others without the presence of the secret escape route, i.e. only relying on exploiting five resource patches.

2.6.4 Familiarity

Familiarity facilitates many interrelated mechanisms like recognition, communication, coordination, aggregation, or reciprocity. Those mechanisms would deserve their own path of direct and indirect effects: for example, coordination can be facilitated by both familiarity (repeated interactions) and communication (sharing social information). Moreover, we could expect communication and coordination to impact different survival-related behaviours or the same behaviours differently. We could not measure communication among players, and thus we could not differentiate it from coordination, or any other mechanism potentially facilitated by familiarity. Nonetheless, we could distinguish prey that can benefit from those mechanisms from prey that cannot and thus allow us to quantify significant opposing effects on survival.

Our study dichotomized familiarity between two prey (two individuals were either familiar or not); thus, a model using a continuous variable based on the strength of the bond or on previous trials could perhaps yield a more nuanced interpretation of the results. For example, familiarity between guppies (*P. reticulata*) and its benefits developed gradually over 12 days, but persisted once established (Griffiths & Magurran, 1997), even after five weeks of isolation (Bhat et Magurran, 2006). Moreover, that long-term familiar (shared youth and adult experiences) dairy cows spent more time together and interacted more frequently (e.g. feeding, resting, allogrooming) suggests that long-term familiarity creates stronger relationships than shorter-term familiarity (e.g. a shared dry-period) (Gutmann *et al.*, 2015). In our system, prey could increase their efficiency in coordinated resource acquisition, altruism, and even predator avoidance as their familiarity with fellow prey (with repeated trials) increases through better coordination and communication. In contrast, observing the benefits of familiarity that do not increase with time would support the hypothesis that the benefits of familiarity are acquired early. It would suggest that communication (very easy to learn in our system) is perhaps more responsible for the benefits of familiarity than other behaviours that require more time to learn (e.g. coordination).

Our research using video games sheds light on a complex series of interrelated hypotheses and predictions regarding the effects of familiarity on individual behaviour in small groups. We found that familiarity had opposing indirect effects on survival. Familiarity increases the number of predator encounters, which decreases prey survival. On the other hand, familiarity increases prey survival by facilitating resource acquisition. Ultimately, familiarity exerts a weak total positive effect on survival. Using a video game as our model system provided us with a near-complete dataset on individual behavior, and on the ecology of interactions, granting us with a large and robust data set, which would otherwise be very costly and logistically difficult to acquire in nature or in the laboratory. Researchers seeking to test evolutionary or ecological hypotheses requiring large datasets that have complex interactions amongst many individuals (e.g. behavioural syndromes: Sih et al., 2004; social network analyses: Wey et al., 2008) should consider video games as a model system

CHAPITRE 3

Untangling the contribution of active and passive group augmentation benefits to the multilevel selection of altruism using a video game

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3.1 Mise en contexte

Contrairement à mes hypothèses, le second chapitre a conclu que l'altruisme avait un effet direct négatif sur la survie du coopérateur dans notre système d'étude. Sous la sélection naturelle, une telle relation mènerait à la disparition de l'altruisme. Ces résultats ont généré une série de questions sur les coûts et les bénéfices de secourir un autre membre du groupe de la mort. L'altruisme est souvent une interaction sociale et complexe qui peut avoir plusieurs bénéfices à court et long terme.

Ainsi, dans ce chapitre, j'ai identifié, mesuré et comparé différents bénéfices et coûts de l'altruisme. Comme le contexte reste le petit groupe et que le comportement altruiste a un effet direct sur la survie des autres membres du groupe, je me suis concentré sur les effets de la taille du groupe. Secourir un autre membre du groupe préserve la taille du groupe et cela peut générer différents bénéfices actifs ou passifs.

Pour tester mes hypothèses, j'ai procédé à une expérience où j'ai fixé un phénotype pur d'altruisme chez les proies (des altruistes vs des non-altruistes). Cette approche a permis d'obtenir des groupes avec différentes fréquences d'altruiste pour mesurer les effets de l'altruisme au niveau individuel et au niveau du groupe.

3.2 ABSTRACT

The group augmentation hypothesis states that individuals gain benefits by increasing group size and is rarely studied because it often overlaps with other evolutionary mechanisms like reciprocity. When rescuing a fellow prey from death, the mere presence of that member in the group can yield different benefits that can be passive like risk dilution or active like delayed reciprocity. We were able to separate the effects of passive and active group augmentation benefits by experimentally manipulating the behaviour of prey (altruist vs non-altruist) in a video game where the costs and benefits of altruism were easily measured. The game pits four players-prey who must acquire resources to survive while avoiding getting captured by a fifth player-predator. We instructed half of the prey players to avoid rescuing other prey, and the other half to rescue when possible. Our data showed that increasing the frequency of altruistic prey in a group increased survival for all group members. Maintaining group size yielded passive benefits like improving resource acquisition and facilitating future rescues. These passive benefits had a higher impact on survival than the active benefits (e.g., being rescued in return through reciprocity). Thus, we were able to support the importance of passive benefits from anti-predator altruistic behaviour using a biologically relevant online video game.

Keywords: Altruism, group augmentation, group size, reciprocity, video game

3.3 INTRODUCTION

Altruistic behaviours, where individuals incur fitness costs to improve the fitness of conspecifics, are difficult to explain when observed amongst unrelated individuals (Clutton-Brock 2009). Nonetheless, evolutionary biologists have identified a handful of benefits accrued by altruists to explain the maintenance of altruism (Nowak 2006) including that altruistic individuals can benefit from the altruism of conspecifics that they helped before (i.e. reciprocity, Trivers 1971), through their effect on the foraging efficiency or safety at the group level (i.e. multi-level selection, Traulsen and Nowak 2006), or simply from being embedded in a larger group (i.e. group augmentation, Kokko et al. 2001). A given altruistic behaviour often yields different types of benefits; for example, male white-tailed ptarmigan's (*Lagopus lagopus*) mate-guarding behaviour might ensure its paternity while also reducing its own predation risk and increasing the foraging rate of its mate (Artiss et Martin, 1995). Another example is that of meerkat (*Suricata suricatta*) mobbing behaviour that deters predators, but also facilitates risk assessment for future mobbing decisions and trains juveniles (Graw et Manser, 2007). Because the different benefits of altruism often occur together and overlap, the reality is probably much more nuanced than what a simple mechanism could explain and identifying the relative importance of each mechanism at play can be challenging (Barker *et al.*, 2017 ; García-Ruiz et Taborsky, 2022 ; Kingma *et al.*, 2011 ; Kramer et Meunier, 2016).

Key predictions for group size to sustain altruism (hereafter group augmentation hypothesis) state that helping increases group size and that being in a larger group provides benefits (Kokko *et al.*, 2001 ; Wong et Balshine, 2011). However, the impact of altruism on group size often yields multiple benefits (Kingma et al. 2014; Kokko et al. 2001) that are difficult to distinguish from each other (Bergmüller *et al.*, 2007). Kingma et al. (2011) reported that purple-crowned fairy wren (*Malurus coronatus*) subordinate helpers feed related and unrelated individuals suggesting that subordinates might accrue indirect fitness benefits (through the success of kin) and actively augment their group size, which is beneficial since new recruits will assist them when they eventually obtain a breeding position. The study by Kingma et al. (2011) illustrates the difficulty of disentangling multiple benefits; in this case, kin selection is intertwined with active group augmentation where the receivers reciprocate the help. Such benefits are often referred to as pseudo-reciprocity (Connor 1986, 1995). However, when an altruistic behaviour impacts the size of the group, it can also generate benefits from the mere presence of the additional group members (i.e. passive group augmentation; Kokko et al. 2001). For example, solitary house sparrows (*Passer domesticus*) recruit conspecifics to share newly found divisible food patches, which lowers predation risk by being in a larger group (Elgar, 1986). Another example comes from pied flycatchers (*Ficedula* *hypoleuca*) that join in mobbing predators with neighbours that cooperated in the past and avoid assisting neighbours that did not (Krams *et al.*, 2008). In that study, direct reciprocity, when individuals preferentially help those who have previously helped them (West *et al.*, 2007), appears to act in concert with passive group augmentation mechanisms since mobbing reduces predation and preserves group size. Increasing group size also facilitates generalized reciprocity where individuals follow the simple rule of 'help anyone if helped by someone' (van Doorn and Taborsky 2012; Gfrerer and Taborsky 2017), which is a mechanism more likely to be ubiquitous in nature than direct or indirect reciprocity because it requires no complex cognitive adaptation like individual recognition or memory. Moreover, benefits from altruistic mechanisms can emerge at multiple levels of biological organization: the action is performed by an individual, but the benefits are reaped by members of the group (Maynard Smith, 1976). Hence, when groups are favored because of their size, then a behaviour favouring an increase in group size can be selected for at the group level (i.e. group selection, Maynard Smith 1976). For example, in the cooperatively breeding Lake Tanganyika cichlid (*Neolamprologus pulcher*), larger groups persist for longer and increase the survival and reproductive success of individuals (Heg *et al.*, 2005 ; Jungwirth et Taborsky, 2015).

Group augmentation is probably more common than reported in the literature. When group size provides benefits, any costly behaviour that increases or maintains group size, like vigilance (Brown 1999), mobbing (Graw et Manser, 2007) or predator inspection (Milinski *et al.*, 1997), can be considered as a group augmentation mechanism. Although ecologists often investigate these behaviours, they rarely frame these as benefits associated with group augmentation (Kingma *et al.*, 2014), even though different benefits should be distinguished when investigating the selection exerted on altruism (Kingma *et al.*, 2014 ; Kokko *et al.*, 2001). Also, following Roberts' (2005) conceptual framework on interdependence, group augmentation mechanisms are resilient to cheaters or non-altruistic group members because altruistic and non-altruistic individuals share a common interest. Garay (2009) also modeled group defense against predators and showed that a helper's survival increases even if the receiver is non-cooperative because group size alone can reduce predation risk. Moreover, benefits accrued through passive group augmentation do not require specialized cognitive adaption (Brosnan *et al.*, 2010 ; Krebs et Hesteren, 1994) since they do not require altruists to monitor the behaviour of conspecifics across repeated interactions (Clutton-Brock, 2009b ; Nowak et Sigmund, 2005). Hence, group augmentation benefits could be possible in a large array of taxa.

Quantifying the relative importance of the different types of benefits of altruism, including group size, requires a large array of measurements over an extended period where individuals cooperate (MacColl and Hatchwell 2004). Such datasets are challenging to assemble in wild or free-ranging populations because observing enough groups, or some members within groups, over the timescales necessary to observe the different benefits is difficult. Measuring the benefits of altruism requires monitoring the behaviour of altruistic individuals and their social partners simultaneously. Consequently, the literature examining the empirical evidence of the benefits of altruism through group augmentation is scarce and mostly covers cooperative breeders (Woolfenden 1975; Bergmüller et al. 2007; García-Ruiz and Taborsky 2022), ignoring a wide array of potential group augmentation mechanisms. For example, tests to explain offspring care by non-kin in the cooperatively breeding bell miner (*Manorina melanophrys*) focused on (and did not observe) benefits through active group augmentation only while ignoring passive benefits (Wright *et al.*, 2010). Hence, we argue that group augmentation mechanisms are likely common in nature and are intertwined with other benefits but are largely ignored.

In this study, we aim to find experimental evidence that group augmentation leads to significant benefits that can drive selection by using a multiplayer video game, *Dead by Daylight* (Céré et al. 2021; Fraser Franco et al. 2022; Santostefano et al. in revision). We manipulate an altruistic behaviour to assess its costs and benefits to compare the importance of active and passive group augmentation and of reciprocity benefits. Multiplayer video games are an ideal study system because they allow us to observe many altruistic events while monitoring the foraging efficiency of individuals and their vulnerability to predation. It is also a model system in which it is easy to set up treatment groups where individuals (humans) behave as directed and, in contrast to mathematical models, we can still observe actual behavioural variation from context-dependent plasticity and cognitive bias. Fixing behaviour as treatment groups in our study allows us to break the feedback loop of altruism where the actual cooperative behaviour, rescuing other prey from death, generates more opportunities for predation and thus for future altruism. We can then focus on measuring the selection on a behaviour based on its actual benefits, and not necessarily bother with its transmission and evolution.

Dead by Daylight is a commercial video game in which a group of four players (hereafter the prey) search for and acquire resources while avoiding predation from a fifth player (hereafter the predator). To survive a trial, prey must collectively gather enough resources to enable an escape route. Predators can capture, injure, and eliminate prey. Prey can be altruistic by rescuing other prey when they are captured by the predator or heal them when they are wounded. Examples of similar anti-predatory cooperative behaviours include male field crickets (*Gryllus campestris*) allowing females to access their burrow first when attacked by a predator (Rodríguez-Muñoz *et al.*, 2011), meerkats collaboratively mobbing an incoming predator (Graw et Manser, 2007) and cooperatively breeding cichlid fish (*Neolamprologus pulcher)* defending non-kin eggs from predation (García-Ruiz et Taborsky, 2022). In our study system, prey helping others can receive different benefits either by being helped in return (direct reciprocity) or by rescuing prey that will continue to collect resources used by the group for survival (active group augmentation). Also, rescuing prey has a direct effect on group size: it maintains the already small group size. Hence, altruism here provides the associated passive group augmentation benefits such as diluted predation, which in turn can lead to faster resource acquisition and overall higher chance of being rescued when captured.

We first quantify the net effect of altruism on the survival of the actor and of its group (the receiver). Second, we identify the cost of altruism for its actor and assess the strength of direct reciprocity, as well as benefits from group augmentation. Finally, we assess the relative importance of reciprocity, active group augmentation, and passive group augmentation in maintaining altruism in the system.

We predict that helping others will reduce survival because it will increase predation risk and take time from resource acquisition while increasing the survival of others. We also predict that, although multiple benefits will emerge from altruism, passive group augmentation will be more important than reciprocity or active group augmentation for survival, because group size is known to have a major impact on predation and resource acquisition (e.g. safety in numbers, Krause and Ruxton 2002), especially when predation is high (Garay, 2009 ; Krause et Godin, 1995). The game also favours passive benefits relative to reciprocity because groups are assembled randomly and trials are short in duration.

3.4 METHODS

3.4.1 The study system

The online horror video game *Dead by Daylight* was launched as a commercial product by Behaviour Interactive (Montréal, Canada) in 2016 [see Céré et al. (2021) for a detailed description of the game]. Briefly, *Dead by Daylight* is a game in which four prey attempt to escape from a closed environment while evading a predator. Escape from the environment requires searching for, and depleting, resource patches; once five resource patches have been fully depleted, two exits can be opened to allow the prey to escape. Each resource patch can be depleted in 90 seconds by a single prey, and faster if two or three prey exploit the same patch at the same time. During a trial, prey can be injured by the predator. Injured prey can be healed by a fellow prey but injured prey leave tracks and make noise that can attract the predator. Prey that have been injured twice without being healed can also be captured by the predator. Captured prey are transported to a prey-handling site and are eliminated from the trial after 3 min. However, captured prey can be rescued from this site by fellow prey before the elimination time elapses. A rescue takes one second to complete but navigating toward the captured prey and avoiding the predator can take a significant amount of time. Whether any prey is injured or captured is public information, but prey cannot communicate verbally with each other and do not know the position or behaviour of their fellow prey (unless acquired visually). The predator has access to sound cues and visual information like tracks on the floor (Fraser Franco *et al.*, 2022) to replace other signals that wild predators have like smells, vibrations, or pheromones. We interpreted rescuing fellow prey as an altruistic action because it increases the probability that the altruist will encounter the predator, while increasing the chance of survival of the receiver (Céré *et al.*, 2021). A trial ends when each prey has either escaped through the exit (i.e. survived) or has been eliminated (i.e. died). The predator has no other imperative than hunting (e.g. sleeping, feeding, defending his territory) and the size of the group of prey can decrease during a trial exclusively based on predation (starting at 4 and possibly ending at 0). On average, trials are 7 min in duration (414 ± 163 s (SD), n trials= 5564).

3.4.2 Experimental design

We selected 1100 volunteer players from the *Dead by Daylight* community to participate in our study in exchange for a reward. We selected participants who had played the game for at least 20 hours to ensure that they could competently play the game and their skills would not change significantly throughout the experimental trials. 200 players were instructed to adopt the role of the predator and 800 players were instructed to adopt the role of the prey. 100 volunteers were not given a specific role so that they could change their role depending on demand during the experiment. Volunteers were asked to participate from home in a minimum of 15 trials to ensure a sufficient sample size. The experiment was conducted between 0900 and 1600 on 8 November 2019.

Many actions in *Dead by Daylight* are rewarded with points that the players can use as currency to acquire items and advantages within the game. In our experiment, however, prey were rewarded with a fixed number of points when they survived and predators were rewarded for each prey they eliminated during their trials. No other behaviour was rewarded. This approach ensured prey optimized their probability of surviving rather than piling up reward points with suicidal or non-survival-related behaviours. These points were given at the end of the experiment; therefore, they were not usable during experimental trials. Furthermore, creating pure phenotypes as a measure of altruism avoided the circular effect of predator's captures creating more opportunities for prey's rescues, which in turn, generates more opportunities for capture since prey are not eliminated. We randomly assigned half of the prey (n=400) to the "non-altruistic" phenotype and instructed them to neither heal nor rescue a fellow prey. The other 400 prey were assigned to the "altruistic" phenotype and instructed to help (rescue and heal) other prey in need. Altruists were further instructed to avoid rescuing captured prey when there was too much risk for them (e.g. in view of the predator) and to search for and acquire resources when no prey needed help. Because all player actions were monitored, we knew if prey performed forbidden actions. Trials in which a participant diverged from that of their assigned pure phenotype were not rewarded and removed from the study. The video game system provides an alternate strategy of survival whereby prey can wait for all other prey to be eliminated and then escape through an exit that then automatically opens (regardless of the resources acquired). Volunteers were instructed not to use this option and instead focus on enabling the exits via resource accumulation. The use of this alternative was monitored, and volunteers lost their reward points if they used it.

For each trial, the game automatically created a group of four random prey-participants and paired that group with a random predator-participant. Because of sampling noise, the number of altruistic prey in a given trial varied from zero to four. Wait-times to begin a game can be considerable because they start only when the correct ratio of predator-to-prey (1:4) is achieved. We circumvented this problem by assigning the necessary number of players from our pool of 100 unassigned volunteers to the "non-altruistic" phenotype. This phenotype was assigned because it was the simpler of the two; fulfilling the single behaviour of never helping. Our experimental design was not fully blinded per se since players knew which phenotype they were asked to display, however they were not aware in which group treatments they were in, i.e. how many altruists was in their group.

3.4.3 Data collection

Of the 1,100 selected players, only 547 participated in the experiment. From those participants, 253 and 294 were assigned the altruistic or non-altruistic phenotype, respectively. 1,493 trials were conducted during the experiment. We first ensured that prey respected their assigned phenotype by filtering any trial in which a non-altruistic prey performed altruistic actions. 1,388 trials met our criteria for inclusion in the final dataset, representing 5,552 focal prey (four per trial). On the other hand, we retained trials where altruistic prey recorded no altruistic actions because they might not have had the opportunity to be altruistic or, if they were, they might not have been successful in their attempt. 36.6% of altruistic prey (1,004 instances of prey in a trial) did not successfully rescue any prey because they either did not encounter an opportunity or failed in their rescuing attempts. For each remaining trial, we recorded the phenotype ('non-altruist' or 'altruist'), the number of other prey with the 'altruist' phenotype in the group (0-3), whether the focal prey survived (0=false, 1=true), and the total number of prey that survived the trial (0-4). The game automatically monitors the location and time of each behaviour performed by each participant in all trials. Thus, it calculates the number of times the predator encounters each prey and the number of resources acquired by each prey. It also records when a prey is captured and/or rescued and by whom. The data recording was automated so unbiased by the fact that we knew the behavioural phenotypes of each individual.

All analyses were performed in the R statistical environment v4.0.2 (R Core Team, 2020) using the lme4 package for mixed effects models (Bates *et al.*, 2015). Means are presented ± 1 SD unless otherwise noted. Below, we describe our statistical approach to meet our four objectives in addition to providing the results for each.

3.5 Statistical analyses

3.5.1 Net effect of altruism

We first measured the overall survival of prey across all trials and tested whether survival differed significantly between altruistic and non-altruistic prey. We then measured the net effect of rescuing other prey on survival at the individual level (actors) and at the group level (receivers) by using contextual analysis (Heisler and Damuth 1987; Goodnight et al. 1992; Okasha 2004). We used a generalized linear mixed model with survival as the binary response variable (0=did not survive; 1=survived) and focal prey phenotype (binary variable: altruist, non-altruist) and the frequency of the altruistic phenotype in the group (ordered variable: 0=no altruists; 0.25=1 altruist; 0.5=2 altruists; 0.75=3 altruists; and 1.0=4 altruists) as independent fixed factors (see model A in Table 3.1). Focal prey phenotype was the individual-level character while the frequency of altruists was the group-level character (based on Okasha 2004). We also included a unique identification number for the predator-player (*predator_id*) as a random effect to statistically control for predator skill. For this analysis, we retained all prey in each trial and included a unique identification number for the trial (*trial_id*) and for the prey (*prey_id*) as random effects to avoid pseudo-replication. In our model, the partial regression estimates of the focal phenotype and the frequency of the altruistic phenotype represented the direction and strength of individual and group-level selection pressures respectively (based on Okasha 2004).

3.5.2 Cost of altruism

We assessed the direct costs of altruism on the actor by first examining whether rescuing captured prey increases predation on the actor, and second, whether it reduces resource acquisition by the actor by using two separate generalized linear models. One model analyzed the number of injuries an individual prey received from the predator in each trial (Poisson distribution) in relation to their phenotype (n=5,552). A second model compared the quantity of resources (Gaussian distribution) acquired by players as a function of their phenotype (n=5,552). In both models, we included the frequency of altruists in the group as a fixed main effect and its interaction term with the phenotype of the focal prey (8 levels). We also added the *prey_id*, *predator_id*, and *trial_id* (as with previous models) as random effects to control for pseudo-replication and to account for differences in predation pressure across trials due to predator skill.

3.5.3 Reciprocity and Active group augmentation

We assessed the benefits of altruism through direct reciprocity by creating a dataset that included cases in which a prey was captured, whether it was rescued, and its phenotype. We then counted the number of direct reciprocity events (i.e. a captured prey was rescued and then subsequently rescued its rescuer later in the trial). To do so, we analyzed the rescues occuring within the first 5 minutes of the trial since reciprocity requires time and opportunity to be conducted. Of those early rescues, we counted the number of times the rescuers were subsequently captured (after the first 5 minutes of the trial) and if they were rescued by the prey that they originally rescued (i.e. a direct reciprocity event).

The benefits of altruism through group augmentation hypothesis assumes that helping others maintains groups at their maximum size for longer periods during each trial. Groups in our study can vary between 4 (at the onset of the trial) and 1. To quantify the effect of altruism on group size, we therefore analyzed the length of time during which all prey were alive (i.e. where group size was at its maximum) as a function of the frequency of altruists in the group (fixed effect) and *predator_id* (random effect) (n trials=1,388).

We identified two potential benefits to altruistic individuals from active group augmentation in our study system. First, prey rescued by an altruistic individual might acquire enough resources after their rescue to impact the survival of the altruist. We tested this prediction by using a mixed effects model analysing the quantity of resources acquired by rescued prey (squared) as a function of the frequency of altruistic individuals in the group (fixed effect) and the identity of the predator (random effect) (n trials =1,388). Second, altruistic individuals could increase their chances of being rescued by helping altruistic group members. We tested this prediction using a generalized linear mixed model to analyze the survival of a focal altruistic prey in each trial (binary variable) as a function of the number of rescues of altruistic prey and the number of rescues of non-altruistic prey that it performed (fixed effects) (n trials =2,748). We also added the number of injuries sustained by all prey in the group to control for differences in opportunities for rescues among trials. We added prey and predator identities as random effects. Finally, we tested if altruists received more help than non-altruists to assess whether altruists were biased in whom they rescued. To do so, we used a binomial model that quantifies the probability of being rescued as a function of the phenotype of the captured prey and the frequency of other altruists in the group, since it has a strong effect on the probability of rescues (instances of captured prey (n)=7,293).

3.5.4 Passive group augmentation

Altruism can be beneficial by increasing the number of group members, thereby diluting the risk of predation, speeding up resource acquisition and easing up rescues. To test this prediction, we split each trial into segments based on the number of living prey (4, 3, 2, or 1) and then calculated the amount of resources acquired as well as the number of predator-related injuries sustained per prey per minute in each segment. We built two separate linear models with either resource acquisition (lm with normal distribution) or injuries (glm with Poisson distribution) as the response variable and the number of living prey or group size (linear and quadratic effects) as an independent fixed effect (n trials=5,547). We also added the *prey_id*, *predator_id*, and *trial_id* as random effects. We built a third model to test the impact of group size on rescues. For each capture of a prey by the predator, we used a binomial model with rescue (0=not rescued, 1=rescued) as the response variable, number of living prey (group size) as the explanatory variable, and duration at each group size as a covariate to estimate the probability of being rescued when captured at different group sizes. For this model, we retained only observations with at least one capture and one altruist alive in the group (instance of prey capture (n) =1,613) and added the *predator_id* as a random effect.

3.5.5 Comparing the mechanisms

After measuring the cost and benefits of rescuing other prey (reciprocity, active and passive group augmentation) independently, we assessed their relative importance in explaining variation in survival. For this analysis, we focused on two active group augmentation mechanisms, the number of times the prey was rescued, and the quantity of resources acquired from rescued prey, whereas the elapsed time before a first prey was eliminated or escaped (as a proxy for group size) represented all benefits from passive group augmentation.

These analyses entailed building a generalized linear mixed model (see basic model B in Table 3.1) like our multilevel model (see model A in Table 3.1) while also including confounding variables. We included the number of injuries sustained by the focal prey and the resources acquired during a trial to represent the cost of rescuing others. We also included the total number of injuries sustained by all prey during a trial to statistically control for changes in overall predation pressure and opportunities for altruistic behaviours among trials. Then, we sequentially ran three models that added one type of benefit at a time to that basic model (see models C, D, and E in Table 3.1). Because each of the three models contained only one hypothesized benefit, we could compare models' fit with the Akaike information criterion and the coefficient of determination to assess the variance in survival that is explained by each type of benefit separately. Comparing models including a specific benefit to a model excluding it would allow us to estimate the importance of that type of benefit. For example, a statistically significant effect of group size would support the passive group augmentation hypothesis. Finally, we ran a full model (see model F in Table 3.1) with all types of benefits and confounding factors. This full model allowed us to check for any indirect effects that were unaccounted for by our hypotheses, for example, if the phenotype or the frequency of altruists still had some significant effect on survival.

Table 3.1 Parameters in each of our survival models (included if marked by an X). Parameters in italics are confounding variables and in bold are the benefits of altruism in *Dead By Daylight*. Model A is the multilevel model. Model B includes control variables and is the reference on which models C, E, and F are compared. Models C, D, and E each include one unique benefit to measure the variance explained by each benefit. Model F is a full model to quantify the variance explained by all hypothesized benefits. Sample size, R^2, and *AIC* for each model are shown at the bottom.

	A. Multilevel model	B. Basic model	C. Rescues model (active GA)	D. Additional resources model (active GA)	E. Group size model (passive GA)	F. Full model
Phenotype	x	x	x	x	x	x
Frequency of altruists	x	x	x	x	x	x
Number of injuries incurred		x	x	x	x	x
Resources acquired by focal prey		x	x	x	x	x
Number of times the focal prey recued another prey		x	x	x	x	x
Number of times all prey got injured by the predator		x	x	x	x	x
Number of times the focal prey was rescued			**x**			x
Resources acquired by rescued prey				**x**		x
Duration as maximum group size (4 prey)					**x**	x
Sample size	5,552	5,552	5,552	5,552	5,552	5,552
R^2	0.089	0.420	0.444	0.427	0.552	0.572
AIC	5270.2	3979.6	3860.8	3965.6	3655.3	3546.7

3.6 RESULTS

3.6.1 Net effect of altruism

The average survival probability of focal prey was 0.279 across all 1,388 trials. The survival of altruists (0.291) was not significantly different from that of non-altruists (0.268) (difference = 0.023, 95% CI = -0.001 – 0.046, χ^2 =3.3997, p = 0.065). As predicted, non-altruistic prey had higher survival probability than altruistic prey when controlling for the frequency of altruists in the group (i.e. altruistic behaviour is favored by individual-level selection; difference in odds ratio = 2.22, CI=1.78 – 2.77, p < 0.001, Figure 3.1a). The survival of focal prey increased with the frequency of altruists in the group (i.e. altruistic behaviour could be favoured by group-level selection; linear effect: odds ratio = 21.58, CI = 11.79 – 39.49, p < 0.001; quadratic effect: odds ratio = 0.73, 95% CI = 0.45–1.18, p =0.194, Figure 3.1a).

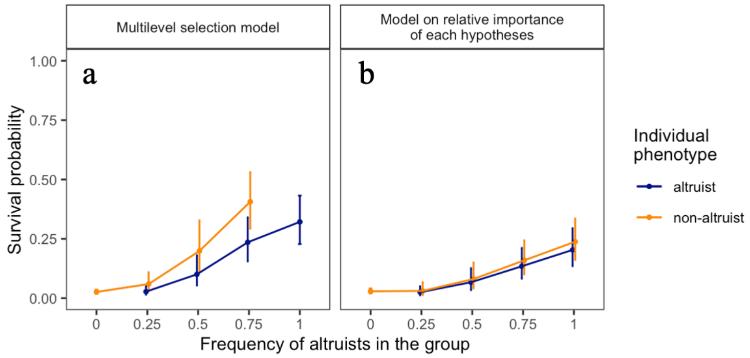


Figure 3.1 Predicted probability of survival for each phenotype (altruist or non-altruist) as a function of the frequency of altruistic prey in the group. (a) the multilevel selection model (individual phenotype and frequency of phenotypes in the group) and (b) the full model including passive and active group mechanisms (individual phenotype, frequency of phenotypes in the group, rescues, resources from rescued prey and group size) (n trials= 5,552).

3.6.2 Cost of altruism

Altruistic prey (2.44 ± 1.50 injuries per trial) were injured significantly more often than non-altruistic prey (1.86 ± 1.27 injuries per trial; incidence rate ratio = 1.19, 95% CI=1.08 – 1.32, p<0.001), which supports our prediction that predation risk is higher for altruists. We found that injuries sustained by prey increased with the frequency of altruists in the group (linear effect = 2.44, CI=2.17 – 2.76, p < 0.001,

Figure 3.2a). A given altruistic prey suffered significantly more injuries as the frequency of altruists in the group increased compared with a given non-altruist [difference in the linear effect of the frequency of altruists between altruists and non-altruistic individuals (odds ratio) = 0.64, CI=0.54 – 0.76, p < 0.001, Figure 3.2a].

Non-altruistic prey acquired more resources (+28.2% on average) irrespective of the frequency of altruists in the group (incidence rate ratio = 1.58, CI = 1.48 – 1.69, p < 0.001, Figure 3.b). Helping others improved resource acquisition as altruistic prey acquired more resources as the number of altruists in their group increased (linear effect (incidence rate ratio) = 2.00, CI = 1.82 – 2.20, p < 0.001, Figure 3.b). This increase was smaller for non-altruistic prey (interaction rate ratio = 0.76, CI = 0.76 – 0.77, p < 0.001. Figure 3.b). In sum, our analyses suggest that altruism is costly as it increases the risk of injury and decreases resource acquisition of the actor.

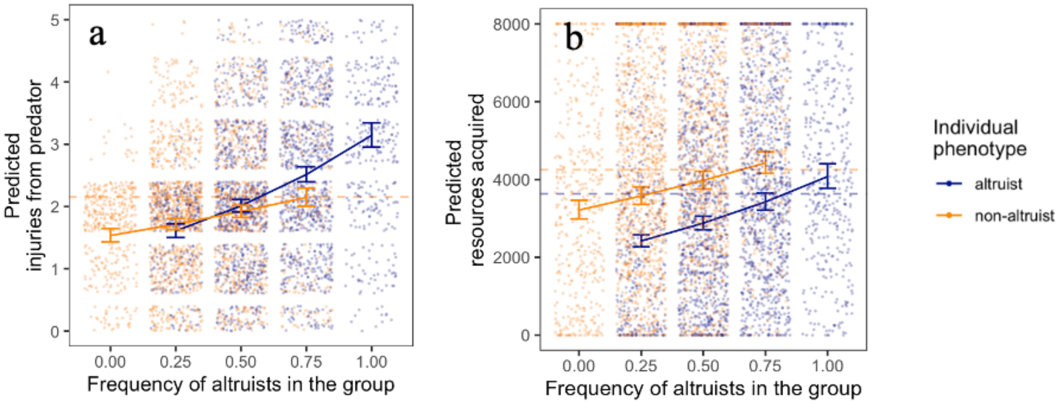


Figure 3.2 Predicted numbers of encounters with the predator (a) and resource points acquired by prey (b) in relation to the phenotype of the focal prey and the frequency of altruists in the group based on a Poisson generalized linear model (n trials=5,552). Dashed lines represent average values for altruists (blue) and non-altruistic (orange) individuals. Data were jittered to avoid overplotting

3.6.3 Reciprocity and Active group augmentation

As predicted, the duration that groups of prey spent at the maximum group size (4 prey) within a trial increased with the frequency of altruists in the group (linear estimate = 207.72, CI = 185.76 – 229.65, p < 0.001), which was responsible for 19.8% (Marginal R^2) of the variation in duration at the maximum group size. On average, groups comprising only altruistic individuals remained at this initial size more than twice as long (408.37 ± 13.68 s) as groups comprising only non-altruistic individuals (200.65 ± 13.55 s). As predicted by the active group augmentation hypothesis, resource acquisition by rescued prey increased exponentially with the number of altruistic members in a group (linear estimate = 32.14, 95% CI = 28.98 – 35.30, $p < 0.001$; see Figure 3.3). In fact, there were 6.6 times more resources acquired by rescued prey in groups with four altruists than in groups with only one altruist.

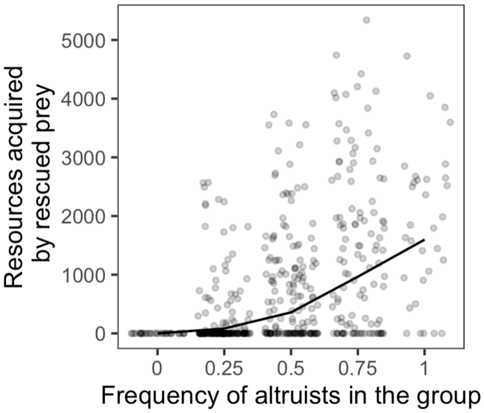


Figure 3.3 Predicted total number of resource points acquired by prey that were rescued as a function of the frequency of altruists in the group based on a Poisson generalized linear model (n trials=1,388)

There was a total of 4,629 rescue events across all trials. 12.6% (n = 585) were instances of direct reciprocity where the prey was rescued by someone it previously rescued. We registered 2,621 instances where an altruistic prey rescued another within the first 5 min of the trial and were captured afterward. Of those subsequent capture, the prey was rescued in 31.4% of instances (n=822). Those rescues were performed by the original rescued prey (i.e. a direct reciprocity event) 35.0% of the time (n=288).

Rescuing an altruistic prey in a trial had a positive impact on the rescuer's survival (odds ratio = 1.74, CI = 1.47 – 2.06, $p < 0.001$), whereas rescuing a non-altruistic prey did not (odds ratio = 0.96, CI = 0.79 – 1.16, $p = 0.660$). Altruistic prey had a higher probability of being rescued (49.6%) than non-altruistic prey (37.3%) (difference between altruistic and non-altruistic prey (odds ratio) = 0.66, CI = 0.59 – 0.73, $p < 0.001$). The frequency of altruistic prey in the group significantly increased the likelihood of a successful rescue (odds ratio = 36.42, CI = 28.02 – 47.33, $p < 0.001$, Figure 3.4).

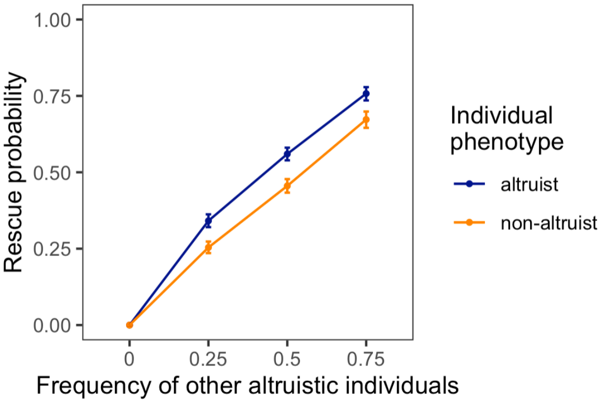


Figure 3.4 Probability of being rescued when captured as a function of the frequency of altruistic prey in the rest of the group based on a binomial general linear model (instances of captured prey (n)=7,293).

3.6.4 Passive group augmentation

As expected, however, prey in larger groups acquired more resources per minute (incidence rate ratio = 3.63, CI = 3.60 – 3.66, p < 0.001; quadratic effect = 0.73, CI = 0.72 – 0.73, p < 0.001, cubic effect = 1.15, CI = 1.15 – 1.16, p < 0.001, Figure 3.5a). Contrary to our prediction, the probability of predator-related injuries for each prey did not decrease as group size increased (incidence rate ratio = 1.11, CI = 0.98 – 1.26, p = 0.104, Figure 3.5b). That result did not change when accounting for player skill (see Appendix D). Also as predicted (Table 3.1), the probability of being rescued increased up to a group size of three (linear odd ratio = 2.01, CI = 1.21 – 3.35, p < 0.007, Figure 3.5c) and then stabilized thereafter (quadratic odd ratio = 0.49, CI = 0.34 – 0.71, p < 0.001, Figure 3.5c); the probability of an individual being rescued was 54% as a member of a group of three compared to 25% as a member of a group of two.

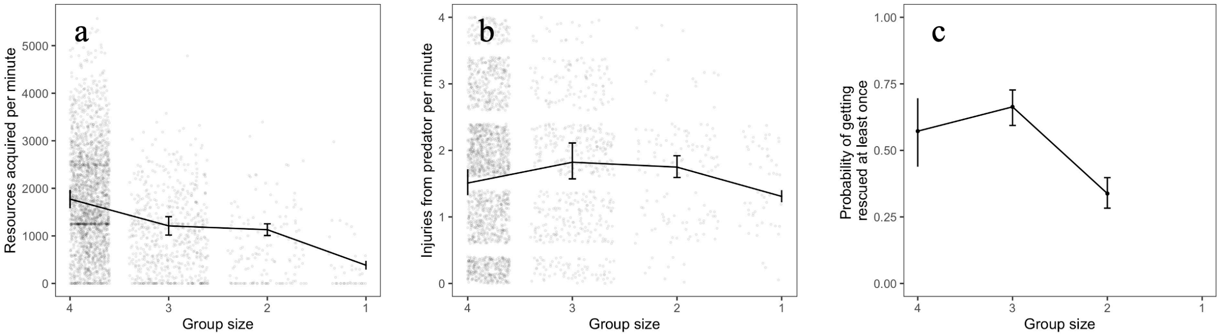


Figure 3.5 Predicted number of injuries from the predator per minute (a) and predicted number of resource acquisition per prey per minute (b) as a function of prey group size based on a linear model (n trials=5,547). Predicted probability of being rescued (c) as a function of prey group size based on a binomial generalized linear model (n trials=1,613). The x-axis is reversed to represent the decreasing group size.

3.6.5 Comparing the types of benefits

We ran three distinct models with each quantifying one possible type of benefit from altruism on survival (see Table 3.1): future rescues (active group augmentation), additional resources from rescued prey (active group augmentation), and group size (passive group augmentation). The group size model (passive group augmentation) that included the length of time during which all prey were alive (our proxy for group size) had the lowest AIC (3655.3, see Table 3.1) and its explanatory factor (group size) accounted for the greatest proportion of variance in survival (13.2%). Hence, passive group augmentation best explains our results as altruism's greatest effect on survival was through its impact on group size. The rescues model (active group augmentation) in which we included the number of times the focal prey was rescued had an AIC of 3860.8 and the number of times the focal prey were rescued from capture accounted for 2.4% of the explained variation in survival, suggesting a weak effect of active group augmentation. The model with the additional resources from rescued prey had the weakest impact on survival, explaining 0.7% of the variation in survival (AIC = 3965.6).

Our full model combining the different mechanisms as well as confounding factors explained 57.2% of the variation in survival (model F in Table 3.1), while the initial multilevel model containing only prey phenotype and the frequency of altruists in the group explained 8.9% of the variance in survival (model A in Table 3.1). Results of the full model did not differ from what other models showed (see Appendix E). It is noteworthy that when accounting for all the benefits of altruism through group augmentation in the full model, the non-altruistic and altruistic individuals exhibited similar survival probabilities (odds ratio = 1.22, CI = 0.89 – 1.68, p = 0.216, Figure 3.1b). However, survival still increased with the frequency of altruistic phenotypes in the group (odds ratio = 7.79, CI = 3.74 – 16.24, p < 0.001, Figure 3.1b).

3.7 DISCUSSION

Our objective in this experiment was to test four mechanisms that explain the maintenance of altruism by quantifying the benefits associated with altruistic behaviours performed by prey under predation in a video game. By monitoring the behaviour and performance of altruistic and non-altruistic individuals interacting under predation we revealed opposing selection gradients for altruism at the individual and group levels. That is, while altruists suffered lower survival due to increasing risk of injury and decreasing resource acquisition, their presence increased the survival of all group members. We supported the passive group augmentation hypothesis by showing that larger groups acquire resources faster and members of larger groups have a greater probability of being rescued. We also found some support for the active group augmentation hypothesis given that members of larger groups have a greater chance of being rescued later through direct or generalized reciprocity. Our results support a key prediction of Kokko's (2001) model on the evolution of cooperation through group augmentation: ‘helping can evolve through group augmentation if larger group sizes yield automatic 'passive' benefits to group members’. Group augmentation is beneficial because group members share a common interest (Roberts 2005) and might be more common in nature than is otherwise suggested in the literature.

3.7.1 Passive group augmentation

Altruistic prey had the same survival rate as non-altruistic prey. However, the survival of all group members increased with the frequency of non-altruistic prey in the group. Non-altruistic prey saw their survival rate increase from 12.4% to 21.3% when the group included one altruistic member compared to none. Thus, all group members benefited from altruistic individuals. Our approach successfully identified different benefits of altruism and the benefits that emerged from the size of the group explained the largest part of the selection acting on altruism in our study system. Passive benefits of larger groups are often neglected by researchers (Wright, 2007 ; Wright *et al.*, 2010) and mostly ignored when dealing with anti-predatory cooperative behaviour. Still, selection on group or population size has been tested many times (Wade, 1977 ; Wade et Goodnight, 1991). The literature states that despite larger groups encountering predators more often than smaller groups, this cost is offset because additional group members dilute predation. For example, mortality from predation decreased as group size increased in the cooperative mongoose *Suricata suricatta* (Clutton-Brock et al. 1999). In our study, we found that individuals in larger groups did not experience fewer predator-related injuries. On the other hand, larger groups did acquire more resources and performed more rescues, which lead to a higher survival of all individuals. It might appear that resource acquisition improves with additional group members while anti-predator vigilance decreases. Although it is common for animals to adjust their behaviour according to the prevailing risk of predation (Lima and Dill 1990), our study unfortunately could not directly test this hypothesis. Although we manipulated the helping frequency and the reward to ensure that players were behaving as intended (maximizing survival), we did not manipulate group size itself, as it was impossible. Instead, effects were estimated using the variation in group size that resulted from predation. A protocol where both helping and group size were manipulated would have given even more robust conclusions. Nonetheless, benefits to survival of maintaining group size are sufficient to explain altruism if this was a live system. We thus advocate for the testing of both active and passive benefits in investigations of all predation-related altruistic behaviours because, as West et al. (2021) highlighted, this is key to explaining variation in the level of altruism within and across species.

3.7.2 Active group augmentation

Kokko (2001) predicted that even if individuals gain no passive benefits, active benefits may provide a reason to augment the group. We found, however, that the benefits that altruists accrue from the active contribution of rescued group members were negligible. Active group augmentation benefits from rescued members in our study system can take two non-mutually exclusive forms: (1) facilitating the eventual rescue of the altruist (possibly through reciprocity), and (2) the acquisition of additional resources by rescued prey that would have otherwise been eliminated (i.e. an increase in foraging efficiency for the group). As predicted, the probability of being rescued when captured increased with the number of altruistic prey in the group: different altruistic prey could attempt a rescue or they could coordinate to increase their chance of successful rescue. We observed cases of direct reciprocity in rescues (12.6% of all rescues and increasing to 35.0% if only accounting for early original rescues). Direct reciprocity was rare, likely because the altruistic prey were not instructed to select who they would help. Another factor for the limited frequency of reciprocity is the randomness of the groups, as it is often proposed that reciprocity needs repeated interactions between actors to be maintained (Axelrod et Hamilton, 1981). Also, the short trial time (on average 7 min) made it difficult for reciprocity to take place because prey might not have had enough time to find the ‘right’ prey to which to reciprocate the help. Longer trials might have generated more direct reciprocity. Generalized reciprocity where prey ‘help anyone, if helped by someone’ (van Doorn and Taborsky 2012; Gfrerer and Taborsky 2017) is a better candidate to explain helping in our system because trials are short and groups are assembled randomly, thereby limiting the potential for repeated interactions among prey. If true, then direct reciprocity might just be coincidental since the group is small. Our result also suggest that the frequency of direct reciprocity (35% when controlling for early rescues) is not different of randomness (1 in 3 prey or 33%). However, when we controlled for injuries (an obligatory event to allow a capture), being rescued had an overall weak effect on survival since being rescued once did not exempt the prey from being captured again. Thus, rescuing an altruist improved survival more than rescuing a non-altruist, which suggests some direct benefit like reciprocity, even if the benefit is small. However, it could also mean that rescuing an altruist increases the chance that he might eventually rescue others (generalized reciprocity) and thus maintain group size. Our analyses did not show that the rescued prey acquired enough additional resources to meaningfully improve survival of the remaining prey. Longer trials or larger groups would probably have led to different results. For example, reciprocity might increase its frequency and impact if trials were longer or if prey were given a choice of who to help and if they could recognize each other in between trials. Reciprocity might also be lower in larger groups.

3.7.3 The cost of altruism

Helping a group member increased the altruist's predation risk compared with non-altruist. This is likely because predators can guard captured prey and use them as lures to attract other prey similar to spiders that lure prey with their web silk (Lai *et al.*, 2017) or ground beetle larvae that lure amphibians with the movement of its antennae and mandibles (Wizen et Gasith, 2011). Other examples include the central American cichlid *Parachromis friedrichsthalii* who feigns death and mimics a rotting fish to attract its prey (Tobler, 2005) and the angler-fish (*Lophius piscatorius*) that baits other fish with its tentacle borne on the top of its head (Chadwick, 1929). Captured prey attract both other prey as well as the predator, just like floral quality attracts both pollinators and their predators (Heiling et Herberstein, 2004). Beyond the individual cost to the altruistic prey, risks of injuries from the predator increased for both phenotypes as the number of altruists in a group increased. This suggests some intriguing relationship between prey (altruistic) interactions and the efficiency and/or behaviour of the predator, which should be investigated in the future. One noteworthy difference of our system with nature is that predators only hunt and do not have tradeoffs with other tasks like avoiding their own predator, managing energy, or protecting their offspring. The game simplifies the predator-prey interaction to a minimum. The predation risk of altruism could have been lower if the predator was sometimes occupied with other fitness-related tasks. On average, altruistic prey also acquired fewer resources than non-altruistic members, probably because they are investing time in helping others. However, both phenotypes acquired more resources as the frequency of altruistic prey increased in the group. Instead of being eliminated, rescued prey can continue to acquire resources. Hence, altruism also had opposing multilevel effects on resource acquisition. Even though altruism is costly for its actor, altruistic prey had the same survival as non-altruists because benefits, mostly from group size, circled back to them at the group level. This finding supports the hypothesis that group augmentation mechanisms can be selected at multiple levels.

3.7.4 Other benefits

When accounting for all the putative benefits of altruism, including the effect that altruists could have on groups through healing of others, the frequency of altruists in a group still significantly improved survival, meaning that there are some benefits (one or more) that are unaccounted for. One explanation is that our proxy for group size (i.e. duration at maximum group size) did not capture all of the benefits that larger groups enjoy perhaps because some relationships between benefits and group size are nonlinear (Blumstein *et al.*, 1999 ; Dehn, 1990 ; Fernández-Juricic *et al.*, 2007). For example, the effect of group size on the probability of being rescued plateaued at three prey. Moreover, it may have been easier to open one of the two exits after the necessary resources had been acquired when multiple prey were still alive (two or three prey could have been sufficient compared to one prey). This effect may have not been accounted for in our measure of four-member group duration. Given that the phenotypes were pure (i.e. they were either altruistic or non-altruistic) and that the groups were randomly created, we doubt that selection of friends (social relatedness replacing biological relatedness (kin) in our study system) or indirect reciprocity based on reputation were responsible for the effects of altruism on group performance (Nowak 2006).

3.7.5 Conclusion

Video games are simplified, yet realistic, ecosystems that are well suited to investigations of altruism (Fehr et Fischbacher, 2003 ; Kingma *et al.*, 2011). We used a video game with clearly defined groups having within- and between-group variation in altruism, and in which we could manipulate a behavioural phenotype to reduce the noise from the feedback loop of social behaviour. We were able to quantify the direct and indirect costs and benefits of altruistic behaviour (Céré *et al.*, 2021 ; Fraser Franco *et al.*, 2022), which is often impossible to do empirically. Our results supported the predictions of the group augmentation hypothesis. We found that group augmentation yielded more passive benefits for survival than active benefits, thereby adding to the scarce literature on passive benefits from altruism. In our study, helping group members allowed altruists to maintain larger groups, which in turn favoured resource acquisition and increased rescue probability. Group size also increased generalized reciprocity. Our results, and the aim of this paper, emphasize the importance of group augmentation benefits to explain altruism. Passive group augmentation benefits might very well be an unmeasured and often overlooked type of benefit for altruistic behaviour in many systems. Another takeaway is that testing multiple hypotheses at once can shed light on complex situation where the explanation is multifaceted.

CHAPITRE 4

Variation in altruism in random groups using a video game

4.1 Mise en contexte

Au travers des deux chapitres précédents, j'ai observé une grande variation dans les comportements altruistes dans notre système. Je me questionne donc sur ce qui explique cette variation et ce qui explique le degré d'altruisme d'un individu à un moment donné. La variation observée peut provenir des différences individuelles (certains individus sont plus altruistes que d'autres) et de la plasticité qui permet à un individu d'adapter son comportement, notamment selon les conditions écologiques et sociales. Enfin, la variation intra- et interindividuelle est souvent fonction de la variation qui se retrouve aussi dans l'environnement social, car un individu va interagir avec différents types de groupes ou de réseaux plus ou moins altruistes. Cette variation impacte le coût et le bénéfice d'aider alors elle peut directement impacter la sélection de l'altruisme.

Dans cet ultime objectif, je tente d'expliquer la variation dans l'altruisme pour identifier les mécanismes derrière l'altruisme. Pour ce faire, je retourne à des observations en ligne, similairement au second chapitre, pour mesurer les comportements non altérés (décisions d'aider ou pas). À la différence des autres chapitres qui se sont concentrés sur ce qui se passe à l'intérieur d'une partie de jeu, j'émets maintenant des hypothèses sur l'effet de l'altruisme entre les parties de jeu.

4.2 ABSTRACT

Variation is a key component of evolution. How behaviours vary within and among individuals can drive the persistence of costly behaviours like altruism. Individuals can differ systematically in their expression of altruism and their expression of altruism can vary in time, for example in response to their social environment or their recent experience. In this study, we aim to identify mechanisms that contribute to the variation in altruism by using a multiplayer video game (Dead by Daylight) in which groups of four prey must escape a predator. We hypothesize that variation in altruism is driven by the stable differences among individuals, by generalized reciprocity ("pay it forward"), and by recent experiences. To do so, we measured within- and among-individual variation in the expression of altruism of prey in small and random groups. Prey can express altruism in this system by rescuing each other when captured by the predator. We found that variation in altruism was greater within individuals than among them and that an individual's social environment strongly affects the level of altruism that they express. An individual's degree of altruism negatively correlates with the altruism exhibited by current group members. Rescuing others is probably a public good game where few individuals should help for the benefit of everyone. Also, only altruistic individuals tended to help more after being in helpful groups. Lastly, learning from recent experience did not have a positive feedback on current altruism.

Keywords: Altruism, cooperation, within-individual variance, among-individual variance.

4.3 INTRODUCTION

Intra- and interspecific altruism is widespread across animal taxa and covers a range of behaviours like sharing resources (Elgar, 1986), raising offspring (Kokko *et al.*, 2002), or collectively fending off predators (Graw et Manser, 2007). Altruistic behaviours can vary considerably within and among individuals in the type and degree of altruism provided (Barta, 2016 ; Komdeur, 2006 ; Moran *et al.*, 2022), and because altruism is an inherently social activity, altruism is often dependent on the behaviour of others.

Within-individual variation in altruism can emerge if individuals are plastic and can adaptively change their behaviour due to, for example, ontogeny (Bruintjes et Taborsky, 2011 ; English *et al.*, 2015), learning (Barfuss et Meylahn, 2023 ; Dridi et Akçay, 2018), or ecological constraints (Griffin *et al.*, 2004). Plastic individuals are variable in their level of altruism, usually in response to stimuli (Barfuss et Meylahn, 2023). In the cooperatively breeding African cichlid *Neolamprologus pulcher,* for example, subordinate females increase their help after the removal of dominant female breeders because the subordinate's probability of inheriting the breeding position increases (Stiver *et al.*, 2006). Western chimpanzees (*Pan troglodytes*) in Taï National Park cooperate to hunt and need extensive training to perform some hunting roles efficiently (Boesch, 2002). Assessing the cost-to-benefit ratio of helping and choosing when to help also relies on recent individual experiences. For example, Schweinfurth and Taborsky (2020) observed that rats (*Rattus norvegicus*) reciprocate help based on their most recent encounters instead of distant ones. When recent altruistic behaviour yields rewards (positive net payoff), a positive feedback mechanism can condition individuals to help (Barfuss et Meylahn, 2023 ; Wolf *et al.*, 2008).

Among-individual variation (difference between individuals) in altruism can arise due to developmental effects, differences in state (Réale et Dingemanse, 2005 ; Sih *et al.*, 2004 ; Wolf *et al.*, 2008) or additive genetic variation (Charmantier *et al.*, 2007). Among-individual variation in animals entails individuals differing in their average display of altruism (Dingemanse *et al.*, 2010). Chimpanzees, for example, have different and consistent roles (driver, chaser, blocker, and ambusher) within an intricate cooperative hunting strategy (Boesch, 2002). In some species, individuals have pure altruistic phenotypes while others are pure-selfish. For example, some female *Polistes dominulus* wasps cooperate to build nests, while others forgo cooperation altogether by colonizing orphaned nests (Starks, 2001). The repeatability of a trait quantifies the proportion of the total variance that is due to differences among individuals (Bell *et al.*, 2009 ; Nakagawa et Schielzeth, 2010 ; Wolak *et al.*, 2012). Individuals can also differ among themselves in their social environment, meaning some might systematically interact with more altruistic individuals than other. Once within and among-variation is accounted for, residual variation represents his ‘intraindividual behavioural variability’ or ‘predictability’ (Jolles *et al.*, 2019). In other words, while plasticity is the responsiveness to certain stimuli, then predictability is the variation around the plasticity level of an individual (Biro et Adriaenssens, 2013).

Within- and among-individual variation in altruism can also emerge as a feedback response to the social environment (Milinski, 1987 ; Schweinfurth et Taborsky, 2020). Altruism is a social activity and so the conspecifics with which a focal individual interacts will vary in their level of altruism, which will, in turn, affect the subsequent altruism of the focal individual and so on (Santos *et al.*, 2008). Most mechanisms allowing the persistence of costly altruistic behaviour often rely solely on the identity of the participants. Positive assortment, the ability of cooperators to interact or group together, was originally said to be essential to the selection of altruism (Hamilton, 1975). The first explanation for the evolution of altruism was based on interactions between relatives (i.e. kin selection, Hamilton 1964; Browning et al. 2012). Then, the group selection hypothesis posits that costly behaviours can be selected at the level of the group when groups differ in their altruism frequency and that more cooperative groups have fitness advantages compared to more selfish groups (Maynard Smith, 1976). Whole adaptive strategies have evolved for individuals to deal with the variation in their social environment: helpers can punish cheaters (Wong *et al.*, 2007), interact with behaviorally similar individuals (i.e. homophily) (Aksoy, 2015 ; Massen et Koski, 2014), develop optimized cooperative strategies like tit-for-tat (Milinski, 1987 ; Schweinfurth et Taborsky, 2020) or rely on reputation to choose whom to help (McNamara et Doodson, 2015 ; Nowak et Sigmund, 2005). Reciprocal altruism is also an evolutionary mechanism that often relies on repeated interactions (Embrey *et al.*, 2018), specifically for direct reciprocity where the receiver of help pays back its helpers by helping them in return (van Veelan *et al.*, 2012). Similarly, interacting regularly with a limited number of individuals, like in a small group, facilitates the maintenance of altruism (Ohtsuki et al. 2006). However, generalized reciprocity is a simpler strategy wherein someone should ‘help anyone, if helped by someone’ or ‘pay it forward’ (Gfrerer et Taborsky, 2017 ; Van Doorn et Taborsky, 2012). Biologically, generalized reciprocity also requires less cognitive ability as individuals do not have to remember who helped them as is the case in direct reciprocity (Pfeiffer *et al.*, 2005). When altruism generates more altruism, a costly behaviour can cascade through a population (Fowler et Christakis, 2010). When interactions are diversified and numerous, or groups are reshuffled regularly, like in a fission-fusion population, then the cooperative behaviour of one individual is indirectly promoted by the behaviour of individuals it had never interacted with. As an example, a public goods game experiment with human volunteers that were organized in sequential random groups found that cooperation can cascade (increase) over three degrees of separation, meaning that the cooperative behaviour between players in a given round was indirectly impacted by the altruistic behaviour of strangers in remote rounds (through intermediate rounds) (Fowler et Christakis, 2010).

On the other hand, altruism does not always directly beget more altruism from others. Some altruistic behaviours yield benefits to the whole group, in a public good game for example, so few must help, and it is better to let others volunteer (Archetti, 2009 ; Hauert *et al.*, 2002). Thus, factors like group size or group composition are critical (Szolnoki et Perc, 2011). In public good games, altruists and non-altruists (cheaters) can coexist in a mixed equilibrium (Archetti, 2009). Helping can also be competitive when benefits are valuable and opportunities are limited, and that can increase within-individual variation. One example of competitive helping is exhibited by cooperative breeders where helpers must pay to stay (Taborsky, 1985).

Our overall goal in the current study is to understand what drives variation in the expression of altruism to identify the concurrent selection mechanisms sustaining the costly behaviour. We test three hypotheses related to the variation in altruistic behaviours (see Figure 4.1). To test our hypotheses, we used data from an online multiplayer video game, *Dead by Daylight*, that replicates the dynamic between a predator and four prey (Céré *et al.*, 2021, 2024 ; Fraser Franco *et al.*, 2022 ; Santostefano *et al.*, 2024) Video games are ideal study systems because they provide large datasets on altruistic behaviour over repeated interactions across random groups of prey. In Dead by Daylight, prey can rescue others when captured by the predator; rescued prey being public goods. Prey are considered to have died if no one rescued them when they were captured. Prey can survive the trial by collectively acquiring enough resources, and subsequently opening an exit, while avoiding elimination by the predator. In game theory terms, our video game represents a situation wherein prey join random groups to play multiple games of social dilemmas (i.e. rescuing a captured prey). *Dead by Daylight* offered us a unique opportunities to explore what drives variation in altruism in temporary and random groups, a notorious structure that limits positive assortment and thus complicate the persistence of cooperation (Fletcher et Zwick, 2004 ; Fontanari et Santos, 2024 ; Hamilton, 1975). Contrary to game theory modelling, however, our video game allows us to capture organic variation that emerges from the behavioural decisions of thousands of live subjects.

We first hypothesize that some individuals are systematically more altruistic than others. The literature showed that, on average, the proportion of behavioural variance in the wild explained by among-individual difference revolve around 0.35 (Bell *et al.*, 2009). Measures of repeatability for cooperative behaviours includes babysitting in meerkats (English *et al.*, 2010) and vigilance in Florida scrub-jay (*Aphelocoma coerulescens*; (Beauchamp et Barve, 2024)).

Second, we seek to explain the contribution of the social environment to the within- and among-individual variation. Plastic individuals can be responsive to their social environment, both as an immediate response to their current group and as a delayed response to their previous group (see Figure 4.1). Thus, our second hypothesis state that an individual should reciprocate help (i.e. increase their level of altruism) if their current fellow group members are cooperative. In that case, reciprocity can be direct (toward its previous helper) or generalized (toward anyone). Generalized reciprocity can also be delayed if increases in altruism is the result of the help received from a previous group (Fowler et Christakis, 2010). Such plasticity should increase the within-individual variation. On the contrary, if the degree of altruism expressed by a focal individual is inversely related to the altruism expressed by their group members, then it is possible that group members are in competition for opportunities to help or that helping is a public good game where helping benefits everyone, so individuals tend to let others take the risks. In contrast, if an individual decreases their help after being in an altruistic group, then a public good game is more likely than competition. Direct reciprocity is an unlikely mechanism for our study system because individuals were randomly assigned to groups, and trials were short so opportunities to reciprocate help directly to a previous helper were rare. Previous work showed that direct reciprocity does happen in *Dead by Daylight,* but it is probably because groups are small (Céré *et al.*, 2024).

Third, we test the hypothesis that the expression of altruism of an individual can be driven by its recent experience. In line with generalized reciprocity, we predict that an individual will be more likely to help in its current group if its altruistic behaviour was reciprocated (i.e. positively correlated) by its previous group members. Also, plastic individuals might learn about the net payoff of helping from their own previous individual behaviour, so an individual who successfully survived their previous trial while helping others, should be more likely to help in the subsequent trial (rescue others more frequently).

Behavioural variation within and among individuals plays a crucial mechanistic role in the evolution of altruism. Testing how systematic differences between individuals, the social environment and positive feedback loop from recent experience will highlight possible mechanisms for the persistence of altruism in a dynamic of temporary and random groups.

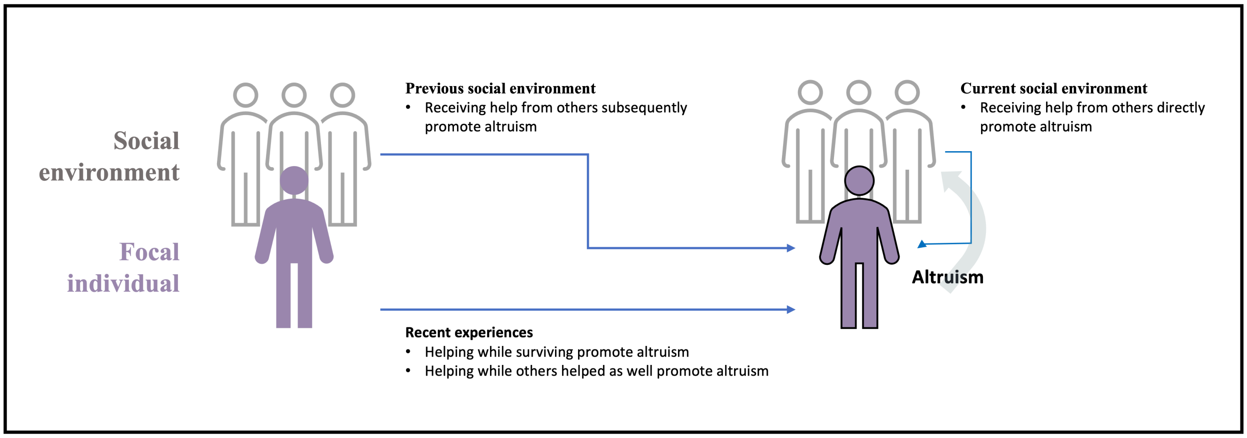


Figure 4.1 Conceptual diagram of our hypotheses on altruism. The purple character represents the focal prey and the grey characters are the other group members. Arrows represent the effect of the help provided over the level of altruism of the focal prey in the current group. Different possible mechanisms are listed concerning whether the effect is positive or negative.

4.4 METHOD

4.4.1 Study system

Our study system is an online multiplayer video game called Dead by Daylight, published in 2016 by Behaviour Interactive (Montréal, QC, Canada) [see Céré et al. (2021) for a detailed description of the game]. The game consists of short trials where one player adopts the role of a predator and hunts four other players (hereafter, the prey). Prey must gather resources from patches and once they have collectively depleted five out of eight patches, they can survive the trial by escaping. A last surviving group member can find and use an alternative escape mechanism rather than meeting the resource-acquisition threshold. The trial duration is, on average, 10.42 ± 4.09 min.

Prey can be injured if hit by the predator. The predator can also capture prey and bind them to one of the prey handling areas. Captured prey can be rescued by fellow prey but are eliminated from the trial after 180 seconds if not rescued (90 seconds if it is their second time being captured). A prey captured for the third time is instantly eliminated. Elimination is regarded as being dead or not having survived the trial. Prey are awarded points when they survive and for any behaviour that they partake in toward survival, including rescues. (Santostefano *et al.*, 2024) found that behaviours like acquiring resources, hiding from the predator, actively engaging in predator defence, and helping others impacted survival via both natural and social selection gradients.

Altruism manifests through one main behaviour: rescuing a captured prey. A captured prey's location is public information so any other prey still alive can attempt a rescue. Altruistic behaviour is both optional and costly to survival since captured prey can be used as bait to capture other prey (Céré *et al.*, 2021). The benefits of helping come primarily from group augmentation where resource acquisition and rescues are facilitated in larger groups (Céré *et al.*, 2024).

Before each trial, the game randomly generates a group of five players with similar skills. Groups of prey can include individuals that are familiar to each other and/or strangers. The population of players at any given time is large enough so that strangers very rarely play with each other more than once. Throughout the manuscript, we refer to the group when discussing strictly social interaction like altruism, but we refer to a trial when addressing non-social related events like survival.

4.4.2 Dataset

We sampled trials from December 2nd to 5th 2022. We randomly selected one focal prey per trial and retained only groups without familiar individuals to avoid the positive effect of familiarity on altruistic behaviour (Céré *et al.*, 2021). For each trial of the focal prey, we considered its previous trial to represent the previous social environment and individual behaviour. We retained focal trials for which the previous trial occurred within 60 min to ensure that the previous experience was recent and to avoid the diminishing effect of time on memory. Trials were retained where the focal prey interacted with entirely different players in its two trials (current and previous). We also filtered out trials with technical issues (e.g. less than four prey, extremely high numbers of interactions). Finally, we kept prey that participated in five trials or more during the sampling period. Our full dataset included 2,248 focal prey in 174,854 focal trials.

Our measure of altruism was the number of successful rescues performed by the focal prey. We also summed up the number successful rescues for the three others prey as the altruism level of the rest of the group. We accounted those values for the current and the previous trials. As opportunities for rescues depend on the predation pressure, we also noted the total number of injuries sustained by all prey in the group.

4.4.3 Measuring variation in altruism

To test our hypotheses, we built three nested binomial generalized linear models (see Table 4.1, models A, B and C) with the number of rescues by the focal prey in the current trial as a poisson response variable. Each models included the total numbers of injuries in the current trial to account for opportunities. The first model (A) included only the ID of the focal prey as a random effect to estimate the among-individual variation in altruism. The second model (B) replicates model A but adds two social environment variables: the sum of rescues from the focal group and the sum of rescues from the previous group. Model B allows us to quantify the proportion of variation that is due to the social environment.

For models A and B, we computed the among-individual variance (V_A) and the repeatability (R) related to the focal prey ID by using the *rptR* package (Stoffel *et al.*, 2017). Confidence intervals are computed via bootstrapping with 1000 iterations. The repeatability (R) represents the proportion of the total variance that can be attributed to among-individual variance (V_A).

The third model (C) allowed us to test our hypotheses on the positive feedback from recent experience. Model (C) the sum of rescues from the focal group and the sum of rescues from the previous group (as in Model B) and added the interaction between the altruism expressed by the focal prey in the previous trial and a binomial variable on whether it survived. This interaction allowed us to test the hypothesis that prey accounted for their recent benefits to adapt their level of help. We also included an interaction between the altruism level of the focal prey and that of the other group members in the previous trial to further explain the impact of the previous social environment and test for the generalized reciprocity hypothesis. Since we include an additional behavioural measure from the focal prey (altruism in the previous trial) in model C, the repeatability (*R*) becomes less representative (bootstrap = 1000 iterations). We also calculate the among-individual variance (V_A). The residual within-individual variation in Model C could be considered as part of the predictability (Jolles *et al.*, 2019).

The three models' fit will be compared with a *Chi-squared* test. We added the *Observation-level random effect* (OLRE) to each model to account for potential overdispersion. These effects explained no variance, so we did not have over-dispersion. We left it out of our analysis because we had the same results either way. We also ran model A with added additional random effects to test for other factors that might influence altruism but without biological relevance (for example: types of character chosen by the prey and the type of virtual environment in which the trial takes place). The full analysis for the Model A is available as supplementary material (see Table 4.2 in Appendix F) but the effects were so negligible that we dropped them from the other models. All analyses were performed in the *R* software (R Core Team, 2020). Means are presented ± 1 SD unless otherwise noted.

4.5 RESULTS

On average, the group of prey were injured 13.09 ± 6.97 (n= 16,272) times and were captured 5.89 ± 3.34 times on average per trial. Focal prey rescued captured prey on average 1.01 ± 1.12 times per trial. Focal prey did not rescue anyone in 42.7% of the trials. 41 prey (1.8 % of all prey) never rescued anyone during all their trials.

Model A included only the identity of the focal prey as a random effect and among-individual differences (*R*) explained 0.079 ± 0.008 of the variance in altruism (see Table 4.1 and Figure 4.2). The repeatability (*R*) was not different when accounting for the social environment in model B (0.071 ± 0.007), and when accounting for the recent experience in model C (0.064 ± 0.007). The total number of injuries explained 17.4 % of the variation in rescues (see Model A in Table 4.1). The explained variance increases to 21.4 % when accounting for the social environment and to 21.7 % when adding the recent experience. Model C had the best fit among the three models [χ^2 = 19.766, DF=4, 40976, p < 0.001].

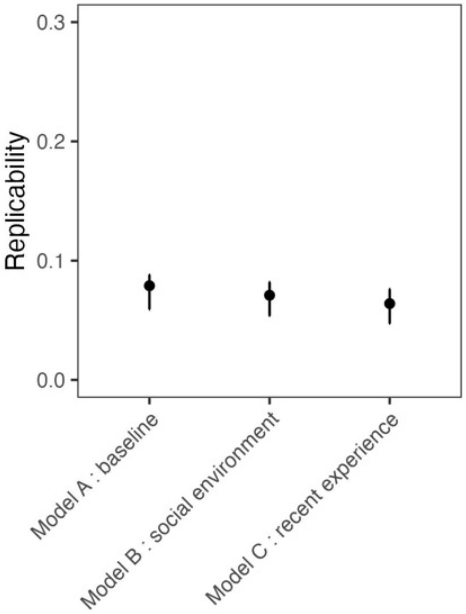


Figure 4.2 The repeatability (*R*) in altruism stayed similar across the three models. n=16,272.

Table 4.1 Variation in altruism explained by our three models having rescues from the focal prey/opportunities of rescues by the focal prey as a binomial response variable. The Focal prey ID is included as a random variable to express the variance explained by among-individual differences. Model A quantifies the among-individual variation in rescues (altruism). Models B and C include the social environment and recent experience, respectively. Estimates for fixed effect are odds ratios with 95% confidence intervals (CI) in parentheses. *p < 0.05. *** p < 0.001. Sample size, R2, and Akaike information criterion for each model are included. Results from additional analysis (Repeatability and calculation for within-individual (residual) variance) are also given. The sample size for all models is n = 16,272.

Interpretation	Variables	Model A	Model B	Model C
Among-individual variation	Among-individual variance (V_A)	0.064 (0.051 – 0.071)	0.053 (0.041 – 0.062)	0.047 (0.035 – 0.056)
	Repeatability (*R*; proportion of among-individual variance)	0.079 (0.059 – 0.088)	0.071 (0.054 – 0.082)	0.064 (0.047 – 0.076)
Within-individual variation	Within-individual variance (V_w)	0.747	0.688	0.689
Random effect	Focal prey ID	0.072	0.053	0.047
Social environment	Total number of injuries	1.50 (1.48 – 1.53) ***	1.78 (1.75 – 1.82) ***	1.78 (1.75 – 1.82) ***
	Number of rescues by others in current trial	-	0.74 (0.72 – 0.75) ***	0.73 (0.72 – 0.75) ***
	Number of rescues by others in previous trial	-	1.02 (1.00 – 1.03) *	1.01 (1.00 – 1.03)
Previous experience	Number of rescues by others in previous trial -by- number of rescues from the focal prey in previous trial (interaction)	-	-	0.98 (0.96 – 1.00) *
	Number of rescues from the focal prey in previous trial	-	-	1.03 (1.01 – 1.05) *
	Survival of focal prey in the previous trial	-	-	1.01 (0.97 – 1.04)
	Number of rescues from the focal prey in previous trial -by- survival of focal prey in previous trial (interaction)	-	-	1.00 (0.97 – 1.04)
	Marginal R^2	0.174	0.214	0.217

Conditional R^2	0.249	0.268	0.266
Akaike information criterion	41884	41005	40994

Contrary to our hypothesis on generalized reciprocity, the number of rescues by others decreased the number of rescues of the focal prey in the current trial [odds ratio 0.73, CI = (0.72 – 0.75), P < 0.001; Figure 4.3]; suggesting instead either a volunteer's dilemma or some competition. The level of altruism of others in the previous trial had no impact on the level of altruism of the focal prey in the focal trial [model C; odds ratio 1.01, CI = (1.00 – 1.03), P = 0.152; Figure 4.3]. The number of rescues by the focal prey was very lightly correlated across the two trials [odds ratio = 1.03, CI = (1.01 – 1.05), P = 0.012]. The relationship between the focal's and the group's level of altruism in the previous trial had a nuanced effect on the current altruism [model C; odds ratio 0.98, CI = (0.96 – 1.00), P = 0.037; Figure 4.4]. When both the focal prey and others helped frequently, then the focal prey tend to help less frequently. However, if he rescued more than others, he tended to continue to be more altruistic. Contrary to our hypothesis on the recent experience, surviving in the previous trial did not impact altruism in the current trial [odds rate ratio = 1.01, CI = (0.97 – 1.04), P = 0.754], nor was there a synergy with the altruism level of the focal prey in the previous [odds ratio = 1.00, CI = (0.97 – 1.04), P = 0.819, Figure 4.5].

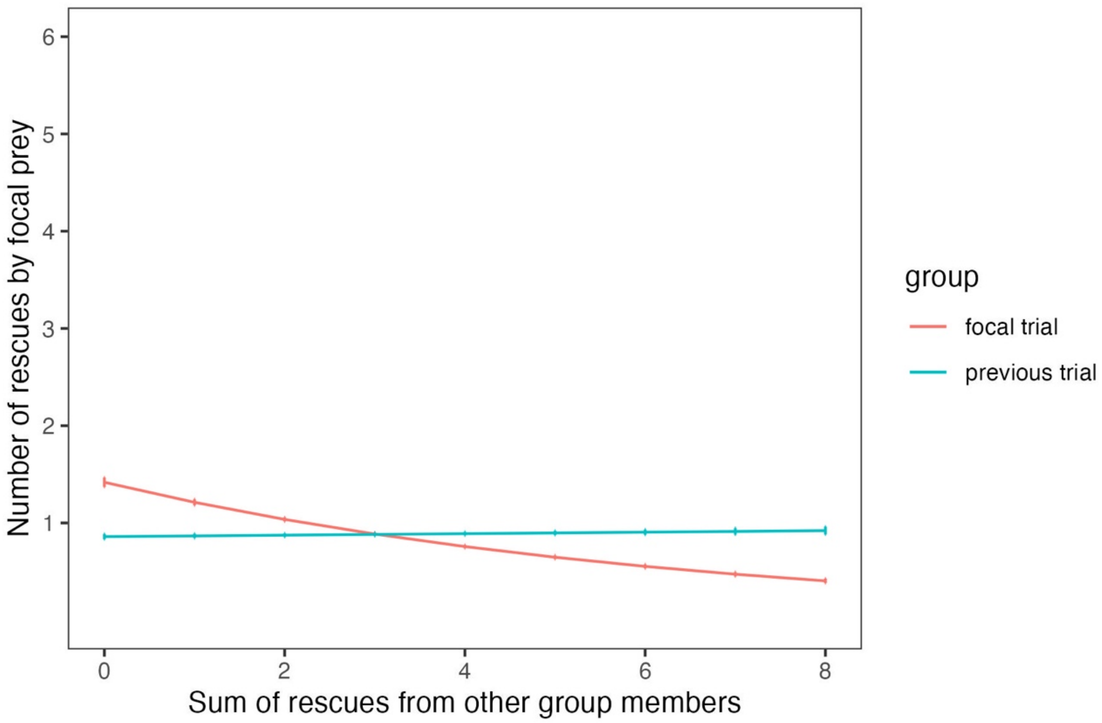


Figure 4.3 Rescues by the focal prey in the current trial directly decrease with the rescues from others in the current trial, but not with the rescues from others in the previous trial . n=16,272.

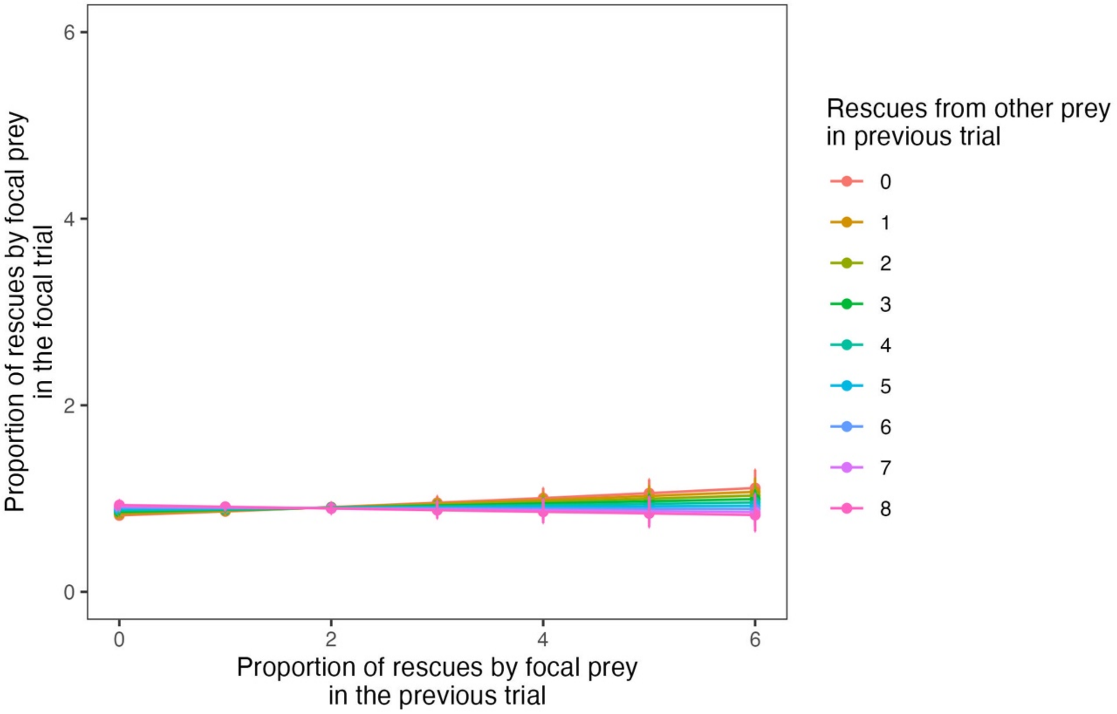


Figure 4.4 Rescues by the focal prey in the previous trial increase the altruism level in the current trial if others rescued rarely and it decreases altruism if others were helpful. Colored lines represent different levels of altruism of the other prey in the previous trial. (n=16,272).

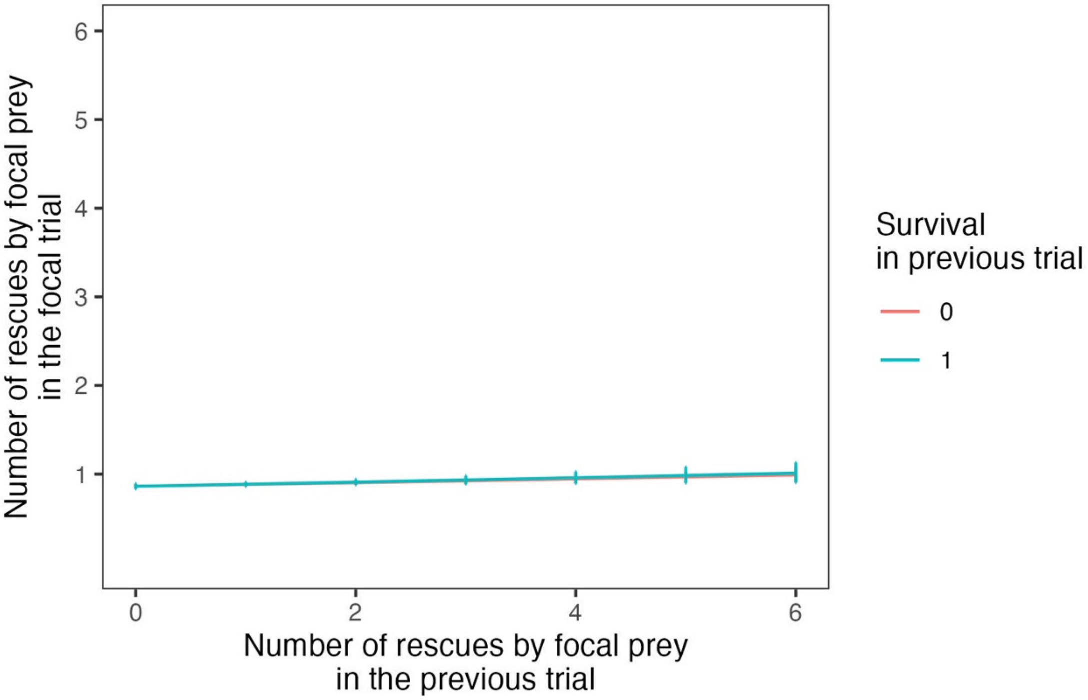


Figure 4.5 The level of altruism of the focal prey in the current trials did not depend on the relationship between having survived (teal line) and having helped in the previous trial. (n=16,272)

4.6 DISCUSSION

In this study, we tested three hypotheses and estimated the variance in altruism within and among individuals to explain how altruism can be selected in temporary random groups. Consistent differences among individuals were lower than what is usually observed in the wild and so within-individual variance was high. Indeed, we found that an individual's expression of altruism was mostly sensitive to opportunities, and to variation in current social groups, such that rescues performed by other group members directly decreased the altruism level of the focal prey. We did not find evidence of generalized reciprocity or positive feedback from helping and surviving in the previous trial. Because rescues benefit all group members in our study system (Céré *et al.*, 2024), our observations of altruism might be best described as a public good game, more specifically a volunteer's dilemma. Altruistic prey made their decision to help, in part, based on the correlation, either positive or negative, between how they previously helped and how helpful their previous group was. Studying the extent and type of variation is essential for testing hypotheses explaining the persistence of altruistic behaviours as it affects its costs, benefits, and evolutionary mechanisms. In total, we were able to explain 26 % of the variance in altruistic behaviour for a given trial, most of it emerging from the number of opportunities. Our findings emphasize the importance of exploring variation (within-, among-individual and across social environments, but also in predictability) when testing hypotheses on the persistence of altruism (Barta, 2016 ; Komdeur, 2006 ; Moran *et al.*, 2022).

4.6.1 Among-individual variation

The altruism level of our focal prey is somehow repeatable across trials, but the effect is very weak and explains only 7.89% of the total variance. This is quite low considering that a meta-analysis on the repeatability of behaviour observed that on average, 35% of the variation can be attributed to among-individual differences (Bell *et al.*, 2009). As a reference, babysitting in meerkats (English *et al.*, 2010) and headturning in Florida scrub-jay (Beauchamp et Barve, 2024) respectfully showed repeatabilities (*R*) of 0.218 and 0.244 respectively. Interestingly, Florida scrub-jay juveniles had a repeatability (0.095) similar to what we observed (Beauchamp et Barve, 2024). The low repeatability possibly suggests that trials were widely different from one to another and that limits prey from expressing consistency in their altruism. Differences between trials can lead to different numbers of opportunities to help and different amplitude of cost and benefits; thus limiting the possibility to behave consistently. Higher altruism-related personality traits could have provided general benefits to actors like task specialization or reduced inter-individual conflict (Bergmüller *et al.*, 2010 ; Jolles *et al.*, 2019). In *Dead by Daylight*, the most cooperative individual might specialize in rescuing captured prey while others concentrate on acquiring resources. Low repeatability can also be a result of a high plasticity (high within-individual variation).

4.6.2 Within-individual variation: the social environment

Contrary to our hypothesis on generalized reciprocity where prey might have 'paid it forward' (Van Doorn et Taborsky, 2012), the altruistic behaviour of current group members had a strong negative effect on an individual's expression of altruism. Limited opportunities to help can explain this negative relationship: others might 'steal' rescues so the focal individual cannot express his altruism at will. This result suggest that rescuing a captured prey is akin to a volunteer's dilemma where one group member's help benefits everyone (Archetti, 2009 ; Diekmann, 1985). In this scenario, it is better to let others pay the cost of helping, but the cost is high for everyone if no help is provided. Findings from Céré et al. (2024) are in line with the description of a public good game because passive group size benefits had the strongest positive effect on survival since all prey acquired resources faster and subsequent rescues were easier before group size decreased (i.e. when captured prey were eliminated). Additionally, the altruism level of the previous group was on its own negligible. However, as shown in model C, prey were more likely to continue to volunteer their help again in their current group if their previous group were not helpful. Prey were also less likely to help if both them and their group were altruistic in the previous group. This decisional algorithm also supports the alternative hypothesis that rescuing in Dead by Daylight is an instance of volunteer's dilemma. Other decisional algorithms include tit-for-tat that maximize reciprocity (Milinski, 1987 ; Schweinfurth et Taborsky, 2020). (Archetti et Scheuring, 2012). We showed that assortment is not required, just as in our random groups, for a volunteer's dilemma to persist. Finally, the negative correlation between the altruism level of individuals further rejects the hypothesis of direct reciprocity.

One other possible alternative hypothesis for that negative relationship in altruism between group members is that group members compete for opportunities to help. In the game, players are rewarded with points (in-game currency to improve their character) if they help, which can be a selfish motivation to compete against others to help. In nature, for example, subordinates in cooperative breeding systems are allowed to stay in the group by helping the dominants (i.e. they pay-to-stay) and will therefore sometimes compete with each other to help (Kokko *et al.*, 2002). However, if competition was the sole driver, prey would not have tended to decrease their help after having helped a lot while being in a altruistic group. Céré et al. (2024) showed that mechanisms were diverse and confounding in Dead by

Daylight: reciprocity, additional resources acquired by rescued prey and passive group size benefits all increased survival to different extents. Thus, the competition and public good game hypotheses are not mutually exclusive.

Adding the social environment to the models improved their predictive power by 4% because it explained some proportion of the within-individual variance. The expectation would have been to observe an increase in repeatability (proportion of the total variance) when the within-individual variance (denominator) decreases by adding explanatory factors like the social environment. However, the repeatability stayed the same for all models. This suggests that there is some difference in social environment among individuals, thus decreasing the among and the within-individual variation at the same time. The most likely explanation comes from the way the game creates groups. The game system accounts, to some extent, for the skill of the players when creating group of strangers. Thus, if there are differences in altruistic behaviour across the range of skills (e.g. skilled players being generally more selfish), then some players are consistently paired up in slightly more altruistic groups than others. Further analyses would be required to test this hypothesis.

4.6.3 Within-individual variation: the recent experience

Consistent differences in average altruism levels between individuals were less prominent than plasticity. Plasticity in cooperative behaviour can be a product of learning whereby individuals adapt their altruistic behaviour according to their previous and current social interactions. Plasticity can also be reinforced with rewards (positive feedback) because individuals can update their perceptions of the current cost and benefits of a given decision based on their recent individual behaviour (Barfuss et Meylahn, 2023 ; Dridi et Akçay, 2018 ; Wolf *et al.*, 2008). We predicted that prey would increase their help after having helped and survived, thus recognizing (or learning) the benefits of helping for survival. However, survival, nor its interaction with altruism, did not incentivize individuals to help more in the next trial. Maybe such learning would have been more important in an experiment including only new players that are still assessing the cost and benefits of altruism.

4.6.4 Unexplained variation

Most of the variation in altruism observed in our study was not explained by our hypotheses. One possible explanation is that there is considerable variation in the cost of helping across trials or even across opportunities within a trial. Rescuing a captured prey with the predator nearby is much riskier than if the predator is not nearby. Studying altruism at the instance level (each captured prey), instead of at the trial level, would allow us to consider different factors (ex.: location, time since the start of the trial, current group size) and might highlight stronger effects. On the other hand, just as it depends on the social group, anti-predatory altruism might heavily rely on the skill or strategy of the predator. Unpublished results from (Céré *et al.*, 2024) showed that the predator's identity accounted for 10.5% of the variance in surviving in an experiment using *Dead by Daylight*. Similarly, Fraser Franco et al. (2022) observed that predators in *Dead by Daylight* display a range of different hunting strategies and individuals portraying predators were flexible between strategies. Thus, the variation coming from the predators might also be an important driver of the variation or the persistence of altruism but studies on the subject are scarce. Being at the right place at the right moment might also be essential for a successful and beneficial rescue (i.e. avoiding the predator and minimizing the trade-off with other tasks; (Céré *et al.*, 2021)), thus making a driver for the expression of altruism as well. Since we only measured successful rescues, we are missing instances where a prey wanted to help but could not, for example, if he realized that the predator was close. Including instances in which the focal individual intended or wanted to help might lead to more consistent measure of the level of altruism, i.e. higher repeatability, and less within-individual variation. We did not measure the among-individual variation in plasticity either, meaning that some individuals might learn faster than others (Wolf *et al.*, 2008) or respond differently to their social environment (Jolles *et al.*, 2019). It is also possible that the learning might be a longer-term mechanism and is less sensible to recent successes or failures. On the other hand, the ultimate benefits of helping may extend beyond survival, such as enhancing one's reputation (McNamara et Doodson, 2015), so responsiveness to previous experience might be linked to other measures.

In future works, game theorists should dissect the situation further because rescuing captured prey in our system, where group size varies, has components from social dilemmas akin to the Volunteer's (Diekmann, 1985), the Prisoner's (Clements et Stephens, 1995) or the Snowdrift dilemmas (Kummerli *et al.*, 2007).

4.6.5 Conclusion

By using data from a multiplayer video game, we were able to estimate how the social environment and recent experience could help explain some of the variation in altruistic behaviour at the among and within-individual levels. We did not find evidence of either direct or generalized reciprocity. However, we found an individual's helping frequency (plasticity) directly depends on its available opportunities and on the level of altruism in their current group. Our study highlights the importance of measuring all sources of variation simultaneously and considering a wide array of mechanisms when studying altruism to present a full picture of how such behaviours emerge and persist under natural selection. Future research should extend our findings by explaining a higher proportion of within-individual variation, such as how plasticity is driven by the variation in the social environment or with differences in individual levels of plasticity or predictability.

CHAPITRE 5

CONCLUSION GÉNÉRALE

Au cours de la présente thèse, j'ai étudié une situation où l'altruisme pouvait potentiellement être sélectionné dans un contexte de petits groupes temporaires et aléatoires. Pour ce faire, j'ai approché l'altruisme et la dynamique de groupe sous différents angles. Le comportement altruiste d'intérêt consistait au sauvetage de proies capturées par le prédateur dans le jeu vidéo *Dead by Daylight*. Je me suis penché sur les liens de familiarité entre les membres du groupe, sur les bénéfices multiniveaux et à la variation dans les comportements altruistes. En synthétisant les différents résultats, on peut conclure que la structure du groupe est centrale dans la sélection de l'altruisme dans notre système à l'étude. La structure en petit groupe affecte la fréquence de l'altruisme en favorisant la familiarité et impacte comment les bénéfices sont distribués entre les membres du groupe. Sauver une autre proie de l'élimination affectait directement la taille du groupe et les avantages passifs émergents bénéficiaient à tous les membres du groupe, soutenant ainsi l'hypothèse de l'augmentation du groupe. Cependant, l'altruisme avait ses coûts sur l'acteur et donc la sélection était double : détrimentaire pour l'acteur, mais bénéfique à l'échelle du groupe. Nous étions donc en présence de sélection de groupe. Comme les bénéfices mesurés sont partagés par l'ensemble des membres du groupe, incluant l'acteur de l'action altruiste, l'altruisme n'avait pas besoin de réciprocité ni d'appariement positif pour persister, deux mécaniques souvent invoquées dans la sélection de l'altruisme. Enfin, c'était plus avantageux pour les proies de laisser les autres sauver les proies capturées, suivant les préceptes du dilemme du volontaire, une dynamique de la théorie des jeux peu étudiée. La principale contribution de la présente thèse est d'apporter du support à plusieurs hypothèses, donc les évidences empiriques sont somme toute limitées dans la littérature : la sélection de groupe, la sélection de l'altruisme dans des groupes temporaires, le dilemme du volontaire et l'hypothèse de l'augmentation du groupe.

Le second chapitre rattachait la familiarité entre les membres du groupe à des comportements liés à la survie (recherche de ressources, sauvetage de proies capturées et évitement du prédateur). La familiarité avait un effet total indirect léger, mais positif sur la survie. Nos résultats ont aussi identifié un effet négatif de l'altruisme sur la survie individuelle de l'acteur; une relation exaspérée par la familiarité qui en augmente la fréquence. L'altruisme affectait la survie de façon directe, mais aussi de façon indirecte en augmentant les rencontres avec le prédateur et en réduisant le temps alloué à l'acquisition de ressources. Ce premier angle a révélé que l'altruisme n'était pas bénéfique pour l'acteur. Cependant, le système incluait une stratégie alternative pour survivre dans l'éventualité où une proie se retrouve seule survivante (c'est-à-dire la trappe). Ainsi, certaines situations existent où il est stratégique d'attendre la mort des autres proies pour profiter de cette alternative, réduisant ainsi les bénéfices nets de l'altruisme.

Pour mieux comprendre les relations mises en lumière lors du second chapitre, j'ai conçu une expérience où j'ai manipulé des phénotypes purs d'altruisme pour un sous-échantillon de joueurs. L'expérience a permis d'identifier une dynamique de sélection multiniveaux soit, la coopération détrimentaire à la survie de l'acteur, mais bénéfique pour la survie de tous les membres du groupe. Les bénéfices passifs reliés à la taille de groupe (taux d'acquisition de ressources plus rapide et sauvetages plus faciles) étaient accessibles à tout le groupe, dont l'acteur du sauvetage. En revanche, les proies altruistes se faisaient blesser plus souvent et acquéraient moins de ressources que les proies non altruistes. Les coûts et les bénéfices des proies altruistes identifiés à l'aide de l'expérience supportaient les résultats observés à l'échelle de la population dans le second chapitre. Au final, un mécanisme d'augmentation de la taille de groupe, sélectionné au niveau du groupe, pourrait donc permettre la persistance d'un tel comportement altruiste dans notre système (Maynard Smith, 1976). J'ai aussi avancé que l'hypothèse de l'augmentation de groupe dans le contexte de stratégies de coopération anti-prédatrices est probablement plus commune que le suggère l'état actuel de la littérature sur l'altruisme. L'augmentation de groupes est souvent ignorée en faveur d'hypothèses plus populaires comme la parentèle ou la réciprocité (Wright, 2007). Contrairement à nos observations du second chapitre, les altruistes n'avaient pas un taux de survie inférieur aux non-altruistes. La trappe n'étant pas une option dans cette expérience, l'altruisme devenait un stratégique plus bénéfique pour la survie.

Enfin, j'ai voulu expliquer la variation interindividuelle et intra-individuelle dans les comportements altruistes. J'ai testé trois hypothèses : (1) des individus sont systématique plus altruistes que d'autres, (2) des altruistes payent au suivant comme proposé par l'hypothèse de la réciprocité généralisée et (3) le niveau d'altruisme dépend de l'expérience récente. Les joueurs démontraient une faible réplicabilité donc les différences systématiques entre les proies (leurs personnalités) étaient limitées. Toutefois, ils manifestaient une plus grande plasticité en réaction au niveau de l'altruisme de leurs groupes actuels. En effet, nous avons détecté une forte corrélation négative entre le degré d'altruisme d'une proie et celui du reste de son groupe. À l'instar d'une dynamique de jeux de biens publics (Archetti, 2009) et à un dilemme du volontaire (Diekmann, 1985), les opportunités de sauvetage étaient limitées et peu avaient besoin de prendre les risques du sauvetage, car les bénéfices étaient redistribués à tout le groupe. Les proies semblaient faiblement réactives aux expériences précédentes pour adapter leur niveau d'altruisme. L'étude a souligné l'importance de la variation à laquelle un individu doit faire face au travers des groupes sociaux auxquels il appartient (Barta, 2016 ; Komdeur, 2006 ; Moran *et al.*, 2022), mais une très grande partie de la variation intra-individuelle reste à expliquer. Étant humain, la rationalité des joueurs leur a probablement permis une meilleure estimation des conditions en jeu et donc, une plus grande plasticité pour adapter leurs comportements par rapport à ce qu'on observe chez les animaux. À cet effet, mesurer des variables environnementales et la prédictibilité des individus (Biro et Adriaenssens, 2013) pourraient être les prochaines pistes d'investigation.

Le système d'étude permettait l'analyse de petits groupes temporaires de seulement quatre individus. Des groupes plus larges auraient présenté des résultats probablement différents. La familiarité entre les membres du groupe aurait été plus faible si la taille du groupe avait dilué les interactions répétées. Il est possible aussi que l'altruisme ait été moins fréquent, car les prédictions du dilemme du volontaire stipulent que l'altruisme diminue avec la taille du groupe, tous s'attendant à ce qu'un autre se porte volontaire (Diekmann, 1985). D'un autre côté, des groupes plus stables auraient généré plus de familiarité et de prédictibilité (Biro et Adriaenssens, 2013) en plus de la spécialisation (English *et al.*, 2015) dans les comportements des autres, augmentant ainsi potentiellement et indirectement la fréquence d'altruisme.

Un des objectifs de ce projet de recherche sur l'altruisme était de choisir des approches holistiques. Dans le second chapitre, j'ai utilisé une analyse de pistes qui impliquait une variété de pistes directes et indirectes sur la survie (Shipley, 2016). Cette approche a identifié plusieurs coûts et bénéfices proximaux et distaux de l'altruisme sur la survie qui sont souvent difficiles à relier dans la nature. De plus, les bénéfices de l'altruisme sont souvent multiples et entrelacés (Wright, 2007). Ainsi, tester une seule hypothèse à la fois donne rarement l'heure juste (Dochtermann et Jenkins, 2011). Dans le troisième chapitre, j'ai donc testé plusieurs hypothèses conjointement en comparant les prédictions des hypothèses de l'augmentation de la taille de groupes passifs et actifs, et les hypothèses liées à la réciprocité dans un contexte de sélection de groupe. Enfin, dans le chapitre 4, j'ai mesuré la variation comportementale de l'altruisme au niveau intra- et interindividuel, tout en incluant l'effet de la variation dans les environnements sociaux. Seulement en se penchant de manière holistique sur les différents éléments en jeu pourrait-on pleinement comprendre comment des comportements sociaux complexes comme l'altruisme ont émergé, persisté et évolué.

En fait, la seconde contribution importante de cette thèse est de présenter les avantages des jeux vidéo comme système d'étude et, par le fait même, poser les bases à une nouvelle approche en recherche sur l'écologie et l'évolution. La recherche a grandement bénéficié de pouvoir suivre des millions d'individus organisés en autant de petits groupes. Un autre avantage non négligeable était d'avoir des mesures d'interactions sociales automatisées et non biaisées par un observateur (Burghardt *et al.*, 2012). De plus, j'ai pu manipuler les comportements d'intérêt pour adresser directement mes hypothèses. Peu de projets de recherches en biologie, et encore moins d'expériences contrôlées, peuvent se targuer d'avoir des tailles d'échantillons aussi grandes (Jennions, 2003).

D'un point de vue scientifique et conceptuel plus global, les jeux vidéo sont des systèmes de simulation extrêmement puissants et versatiles. L'utilisation des jeux vidéo permet donc d'observer des situations difficiles ou impossibles à étudier en nature ou même en laboratoire. Montiglio et al. (2025) propose, entre autres, les jeux vidéo pour étudier les rôles de la compétition et de la prédation comme agent de sélection, la variation comportementale dans les interactions écologiques et la spécialisation individuelle. Plus encore, on peut créer et tester des dynamiques qui n'existent pas nécessairement en réalité pour explorer diverses possibilités en écologie et en évolution, dépassant ainsi ce que la nature actuelle peut nous apprendre. Un des défis importants de la science est de rallier les prédictions qui émergent de la théorie et de la modélisation à des observations empiriques, soit dans la nature ou en laboratoire. Ce défi émerge de nos limites en temps et en ressources, mais aussi des différences conceptuelles entre ces deux dimensions de la recherche. Les jeux vidéo, en tant que représentation de ce que peut être le réel, sont tout indiqués pour servir de pont et ainsi, arrimer et nourrir ces deux dichotomies (Montiglio *et al.*, 2025).

Les jeux vidéo en tant que système d'étude ont aussi leurs limites. Premièrement, les comportements prennent place au sein d'univers imaginés par des concepteurs de jeux. La liberté dans les actions possibles s'inscrit donc à l'intérieur d'une suite de règles définies. Un chercheur doit bien comprendre ces règles pour identifier quelles hypothèses peuvent être testées avec précision et lesquelles sont moins appropriées. Heureusement, le marché offre maintenant une très grande variété d'univers de jeux et peu d'hypothèses peineront à trouver l'environnement de jeu pertinent. Comme les partenariats entre l'industrie et les groupes de recherche sont en croissance, il est probable que l'accès aux données soit plus facile dans un futur proche. Finalement, choisir le bon système d'étude, que ce soit un jeu vidéo ou une espèce animale, est toujours un défi, car chaque option a ses bénéfices et ses limites (Swearengen, 2018).

Les individus à l'étude (humains) peuvent être une autre limite des jeux vidéo. Les motivations, qui sont souvent limpides chez les animaux (survie et reproduction), sont plus floues chez les joueurs de jeux vidéo. Heureusement, les objectifs du jeu *Dead by Daylight* s'arrimaient très bien avec mes hypothèses. Toutefois, certains joueurs peuvent déroger des objectifs proposés par le jeu et agir de façon contre-intuitive. Comme stratégie pour limiter les déviations dans ce que les joueurs tentent d'optimiser, j'ai modifié certaines récompenses dans l'expérience (chapitre 3) : les joueurs étaient récompensés seulement s'ils réussissaient à survivre. Cela dit, les comportements non souhaités sont somme toute rares à l'échelle de la population de millions de joueurs. De plus, en mettant l'accent sur mesurer les conséquences des décisions des joueurs, on peut contourner les postulats rigides du pourquoi ils prennent ces décisions. En conclusion, plusieurs limites existent pour quiconque veut utiliser les jeux vidéo en recherche, mais elles sont surmontables et n'excèdent pas les bénéfices. Je réitère donc que les environnements virtuels comme les jeux vidéo ont un potentiel scientifique énorme pour une grande variété de disciplines, tant en biologie que pour d'autres domaines.

Pour l'instant, le jeu vidéo *Dead by Daylight* supporte les travaux de plusieurs chercheurs en comportement animal (Fraser Franco *et al.*, 2022 ; Santostefano *et al.*, 2024). Une piste pour l'avenir serait de diversifier les hypothèses testées à l'aide de jeux vidéo. L'écologie des populations et des communautés pourrait bénéficier de grands échantillons hétéroclites de joueurs qui évoluent dans le temps. Les modélisateurs de la théorie des jeux pourraient valider plusieurs prédictions sur la résolution de conflits (Quiñones *et al.*, 2016), les interactions prédateur-proies (Moore et Biewener, 2015), ou les stratégies alternatives de recherche de ressources (Vickery *et al.*, 1991). Les jeux dont les joueurs s'associent eux-mêmes en groupe pourraient intéresser les chercheurs en choix de partenaires (Schino et Aureli, 2016). Enfin, les décisions d'un joueur sur le long terme pourraient s'apparenter aux études sur les traits d'histoire de vie (Nylin et Gotthard, 1998). Diversifier les jeux utilisés dans la littérature scientifique donnera aussi du poids pour pleinement convaincre la communauté scientifique des avantages reliés à cette approche.

Pour ce qui est de l'altruisme, la suite des présents travaux pourra prendre différentes avenues. Premièrement, la variance intra-individuelle dans les comportements altruistes qui restent non expliquée suscite plusieurs interrogations. Investiguer la variation interindividuelle dans la plasticité ou mesurer la prédictibilité pourrait en expliquer une partie (Jolles *et al.*, 2019 ; Wolf *et al.*, 2008). Une autre piste pour des travaux futurs repose sur l'échelle à laquelle on étudie l'altruisme. Chacun des designs expérimentaux de cette thèse reposait sur des mesures à l'échelle d'une partie de *Dead by Daylight*. Comme par exemple, j'ai compté la fréquence de sauvetages et de rencontres avec le prédateur dans une partie de jeu complète. L'ultime bénéfice était même la survie au terme de la partie. Une approche alternative serait d'investiguer les comportements d'intérêt à l'échelle de l'occurrence. Que se passe-t-il quand une proie est capturée? Combien de membres du groupe s'approchent pour tenter un sauvetage? Combien de tentatives de sauvetage réussissent au prix de la vie de l'altruiste? Combien de temps une tentative de sauvetage enlève à d'autres impératifs comme la recherche de ressources? Peut-être que cette granularité plus fine dans les questions donnerait des réponses à des échelles plus larges, notamment sur la grande variation intra-individuelle. Les mêmes types de questions pourraient se poser pour les occurrences où le prédateur poursuit une proie.

Parlant de prédation, elle a été centrale tout au long de cette thèse. Le comportement altruiste à l'étude repose sur la capture par le prédateur. Le prédateur détient donc surement plusieurs réponses expliquant la variation intra-individuelle de l'altruisme. Les joueurs-prédateurs n'ont pas tous les mêmes compétences ni les mêmes stratégies de chasse (Fraser Franco *et al.*, 2022). Un prédateur efficace capture plus de proies, et donc génère plus d'opportunités de sauvetage. Un prédateur plus efficace ou un prédateur utilisant une tactique d'embuscade augmente probablement les risques directs pour les altruistes. Il est même possible que ces mêmes prédateurs plus compétents diminuent les bénéfices des sauvetages réussis. C'est donc une avenue d'étude présentant un fort potentiel pour expliquer plus en détail la variation dans l'altruisme, mais aussi dans les comportements anti-prédateurs ou de recherche de ressources. L'effet du risque de prédation sur la coopération a été plusieurs fois étudié (Garay, 2009 ; Krams *et al.*, 2010 ; Milinski *et al.*, 1997), mais dans quelle mesure différentes stratégies de prédation permettent la sélection de comportements altruistes est très peu représenté dans la littérature.

Finalement, la stratégie alternative de survie représentée par la trappe qui s'ouvre pour la dernière proie survivante introduit un dilemme additionnel. En plus de la stratégie altruiste, les proies peuvent prendre une approche égoïste pure en négligeant les ressources et attendre l'élimination des autres pour tenter leur chance avec la trappe. Alternativement, une proie peut choisir une stratégie mixte; par exemple, secourir les premières proies capturées, mais choisir de ne pas aider quand le groupe devient plus petit et la trappe commence à être une stratégie viable. Des modélisateurs de la théorie des jeux pourraient cartographier les différentes stratégies, proposer des prédictions sur la persistance de l'altruisme dans un tel dilemme et tester directement ces prédictions avec les données du jeu vidéo.

APPENDICE A

Dead by Daylight : the study system

The study system

Each trial (or match) of *Dead by Daylight* begins when five players (four prey and a predator) are selected and grouped; trials end when every prey has either been eliminated or has escaped. Trials last on average 10 minutes but there is no time limit. By default, players (prey) in each trial are randomly assigned to a group with three other strangers of similar skill. Prey can also actively pair themselves with one to three friends (familiar individuals). Therefore, groups of prey can be composed of four strangers, four friends, or a mix of both. Any focal prey can have between zero to three familiar individuals in his group. The predator is never familiar to any prey in a trial. The game offers no way of vocal or written communication between group members during a trial but it is common for friends to use external software to communicate while playing. In a survey conducted by *Behaviour Interactive*, 97.5 % of 6,496 players said that they use external software to communicate while playing online multiplayer games like Dead By Daylight with friends.

Data are automatically recorded by the system and stored on an online server. Our data were recorded during a five week period (September 14th to October 17th) in 2018. Data include measures of behaviour, performance and social connections between prey. Players receive points for their behaviour in multiple contexts (foraging, predator-avoidance, cooperation). At the end of every trial, the behaviour of each player in each context is represented by a continuous value score ranging from 1 to 2500.

Before each trial, the game system generates a unique map. The setting (abiotic environment) is poorly lit and offers cover in the form of trees, rocks, walls, and hills. The resource patches that the prey must find and exploit, as well as the prey-handling site where the predator takes his captured prey, are uniformly distributed in the environment.

Behaviours of prey

Foraging

In our system, a prey's behaviour generally comprises foraging, predator evasion, and a suite of altruistic behaviours. First, a prey must forage for resources, (e.g. search for resource patches and exploit them). The main goal of the prey in this video game is to collectively exploit five out of the eight resource patches in the environment. Thus, foraging is the default behaviour, meaning that it is the behaviour that prey perform when no other external pressure is placed on it (i.e. increase predation risk). It is possible for prey to spend the entire trial foraging.

Prey are awarded points for any time spent actively exploiting patches; it is easy to quantify the ability of any prey foraging (variable: *foraging*). Multiple prey can forage the same patch at the same time to exploit a patch is faster. Prey are rewarded points for any second spent in the context of social foraging (variable: *social foraging)*. Once five out of the eight resource patches of the trial have been fully exploited, two exits open and prey can escape the trial (and survive).

Predator avoidance

The second way of behaving is avoiding the predator. Vigilance, fleeing or hiding are behaviour that are assumed to be time trade offs to other activities such as foraging. Any action by the prey (fleeing, exploiting the patches, helping others) can create noises that can attract the predator. The prey cannot injure or eliminate the predator. Prey have three health states: healthy, injured and incapacitated (described below). At the beginning of each trial, the predator can choose one of eight different special abilities (associated with different characters) that will define their hunting strategy (example: placing traps, invisibility, teleportation).

The predator can look for tracks or signs of prey presence. When spotting a prey, the predator pursues it as it can run faster than prey. The number of pursuits (variable: *predator-prey encounters*) a prey is involved in during a trial is our proxy for predator avoidance; the lower the number, the greater the predator avoidance. The predator can hit the prey and injure it; a prey with the *injured* status can behave as a *healthy* prey but it constantly makes noise and leaves tracks. If the predator hits the prey a second time, that second blow will cause the prey to drop on the floor. A prey with the *incapacitated* status cannot do anything besides move slowly, and in doing so, it leaves tracks. The predator can then pick up the prey and take it to a prey-handling site. The prey is then immobilized and a countdown starts whereby the prey is eliminated from the trial after 180 seconds. When prey are captured a second and third time, the countdown is decreased to 90 and 0 seconds, respectively. Another prey can free a captured prey from the prey-handling site before the countdown ends. The captured prey can also try to free itself from the prey-handling site but the probability of success is 4% and failing means accelerating the countdown.

Cooperation

In addition to foraging and anti-predator behaviour, prey can also heal an injured prey or free a captured prey. By definition, altruistic actions are costly to the actor and beneficial to the receiver (West et al. 2007). Receivers of altruism benefit because it increases their probability of survival: being freed from the prey handling site allows prey to stay in the trial and being healed to a better health state allows prey to move more freely and stealthily. Altruistic behaviour is risky since injured prey make noise that can attract the predator and captured prey are often used as bait, so approaching prey in need increases predation risk for the helper. Individuals are awarded points for any successful altruistic action (variable: *altruism*).

APPENDICE B

Path analysis: the complete model

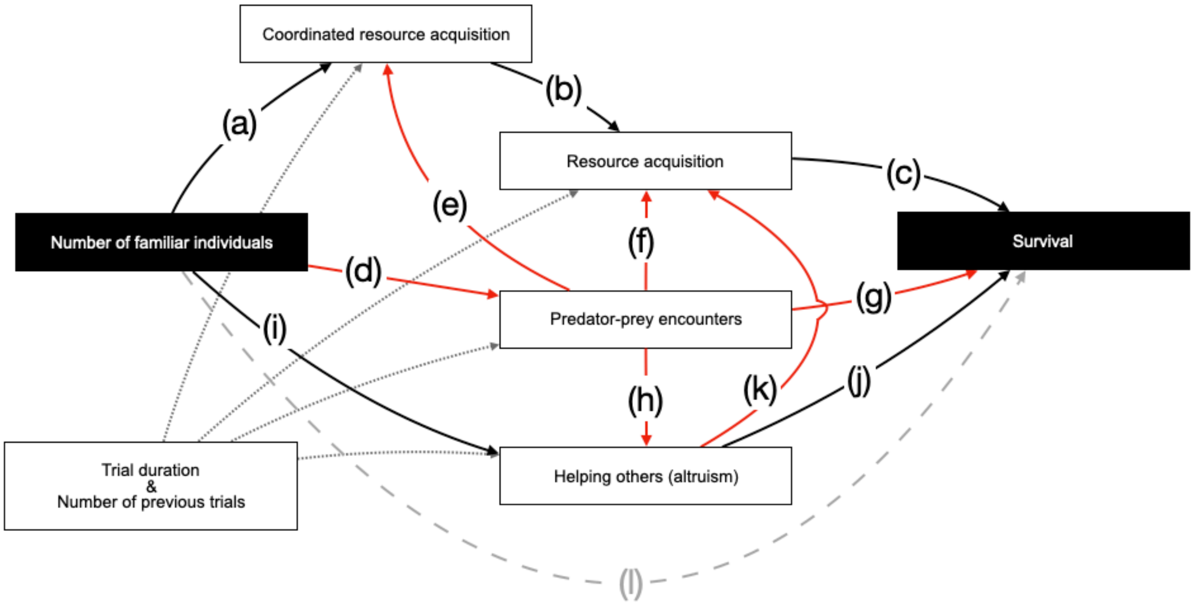
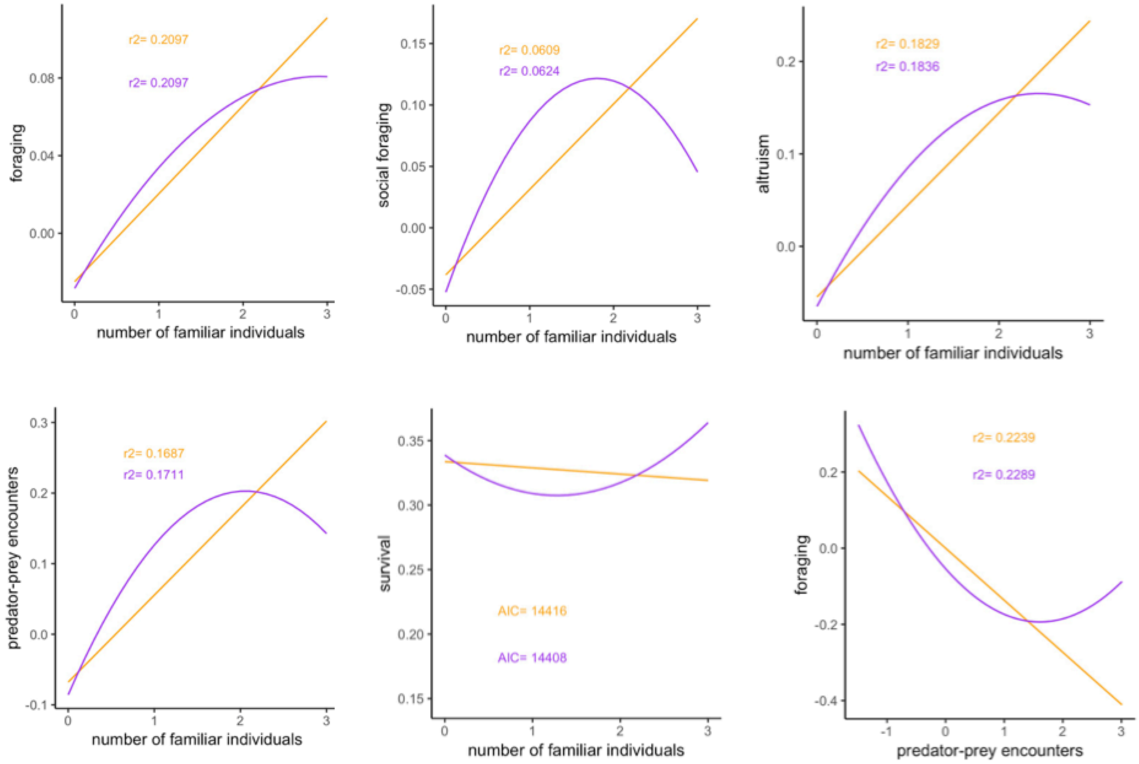


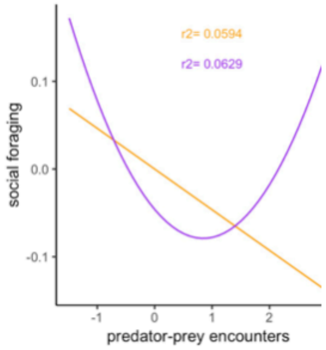
Figure 2.6 Predicted paths of behavioural traits of prey in our system according to our three alternative hypotheses. Solid lines represent the indirect effects of familiarity on survival through social foraging, predator avoidance, and helping others. Black paths represent positive effects and red paths are negative effects. The dashed line represents the residual effect of familiarity on survival. Dotted lines (for trial duration and number of previous trials) are the paths we controlled for.

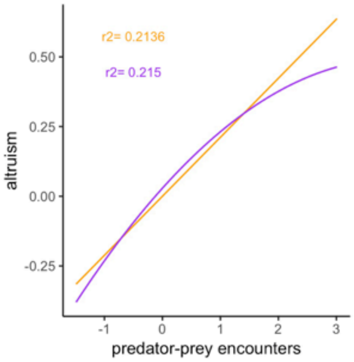
APPENDICE C

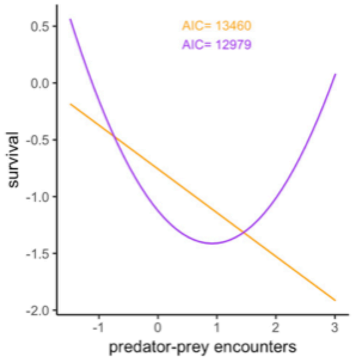
Linear and quadratic relationships for path analysis

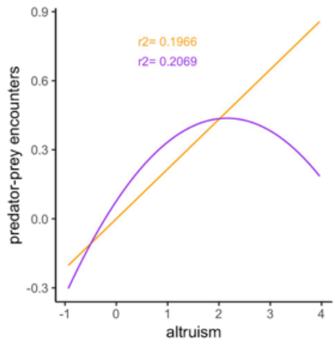
Figure 2.7 Linear and quadratic relationships between variable used in the path analysis. The r^2 from each model (linear and quadratic) are added. The duration of the trial and the amount of previous trials for the prey were added a cofounding variables. No quadratic relationships gave a significantly better fit.

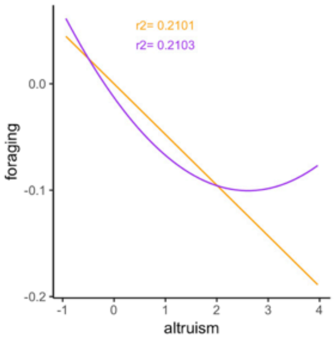


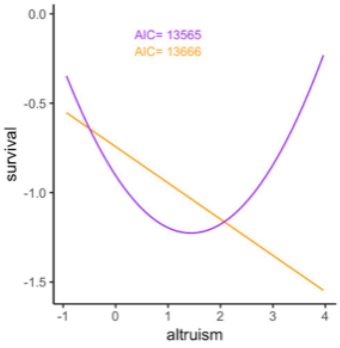

r2= 0.0594
r2= 0.0629
social foraging
0.1
0.0
-0.1
-1
0
1
2
predator-prey encounters

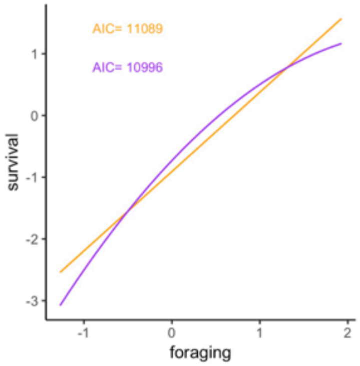

r2= 0.2136
r2= 0.215
altruism
0.50
0.25
0.00
-0.25
-1
0
1
2
3
predator-prey encounters

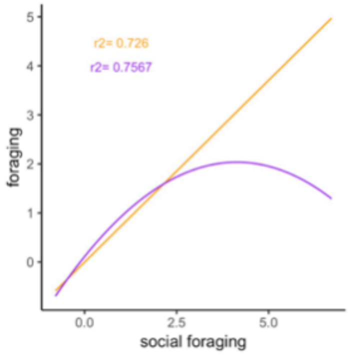

AIC= 13460
AIC= 12979
survival
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-1
0
1
2
3
predator-prey encounters


r2= 0.1966
r2= 0.2069
predator-prey encounters
0.9
0.6
0.3
0.0
-0.3
-1
0
1
2
3
4
altruism


r2= 0.2101
r2= 0.2103
foraging
0.0
-0.1
-0.2
-1
0
1
2
3
4
altruism


AIC= 13565
AIC= 13666
survival
0.0
-0.5
-1.0
-1.5
-1
0
1
2
3
4
altruism


AIC= 11089
AIC= 10996
survival
1
0
-1
-2
-3
-1
0
1
2
foraging


r2= 0.726
r2= 0.7567
foraging
5
4
3
2
1
0
0.0
2.5
5.0
social foraging

APPENDICE D

Skills and group size

We estimated the skill of each player by calculating their individual survival rate and the average number of injuries that they received (see Figure 3.6). However, to infer an impact on their performance in a specific trial, we calculated those values while excluding the specific trial. Hence, for each trial, each player has a survival rate and an average number of injuries that represented his skill in all his other trials.

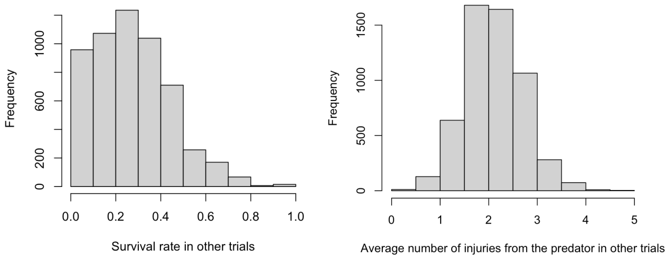


Figure 3.6 Distributions of the estimations of individual skills : survival rate (lefthand side) and average number of injuries in other trials (righthand side).

If those values of skill impacted group size, we would see a difference in skill between groups of different sizes. For example, skills of players in smaller groups (down to two or one prey) would be higher than the skills in larger groups. An analysis of variance showed no statistical difference in the survival rate between groups of different sizes (Figure 3.7; F(3, 5525) = [1.27], p=0.283). A second analysis of variance on injuries in their other trials showed a single significant difference: players in groups of one (lone survivors) received significantly less injuries on average in their other trials (Figure 3.7; F(3, 5525) = [9.132], p<0.001). We wanted to easily capture a possible non-linear effect so opted for analysis of variance where the group size is approached as a discrete variable.

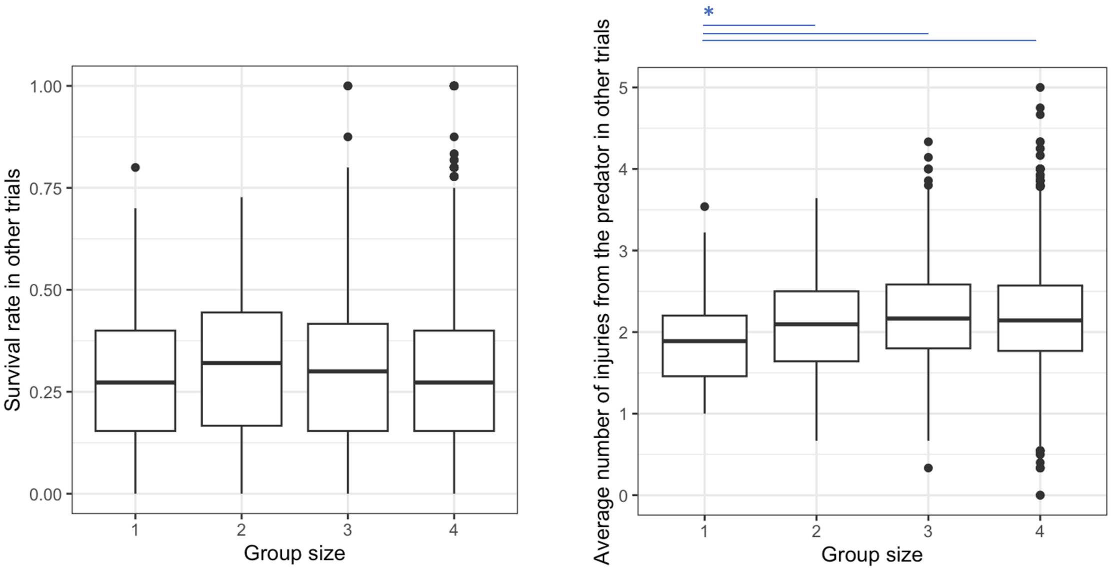


Figure 3.7 Distributions of the estimations of individual skills of prey in groups of different size : survival rate (lefthand side) and average number of injuries in other trials (righthand side).

To push our investigation further, we re-ran our model that investigate if injuries differ between groups of different sizes (passive augmentation benefit related to predation risk) described in the "*passive group augmentation"* method section (glm with a poisson distribution with the *prey_id*, *predator_id*, and *trial_id* as random effects) and shown in Figure 3.5. However, we included the average number of injuries that they received in other trials as a covariate to if it changes the predictions. We don't see a significant difference between the model with and the model without the skill estimation (Figure 3.8).

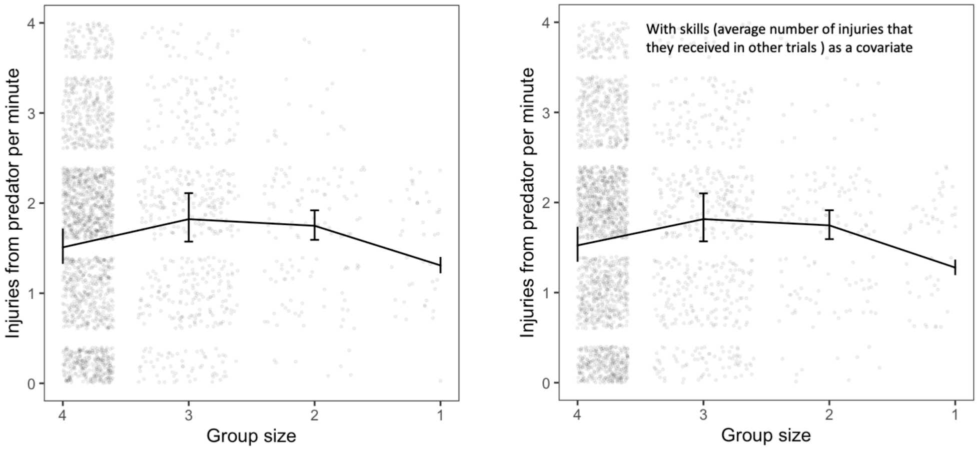


Figure 3.8 Predicted number of injuries from the predator per minute a function of prey group size based on a linear model (n trials=5,547). The x-axis is reversed to represent the decreasing group size. The right-hand panel includes the estimation of skill as a covariate.

APPENDICE E

Contextual full model

Table 3.2 Contextual models (multilevel and full) analyzing the probability of survival. Terms significantly different from 0 are in bold. Odds ratios are exponentials of the coefficients. The phenotype term is the difference in effect of the non-altruistic phenotype compared to the altruistic phenotype. Differences in marginal R^2 are the difference in R^2 between the basic model (phenotype, the frequency of altruists and the cofounding variables) and a model including the same terms in addition to a predictor associated with one group augmentation benefit: number of rescues, resources acquired by rescued prey and group size.

	A. Multilevel model			B. Full Model		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
(Intercept)	0.09	0.06 – 0.13	**<0.001**	0.07	0.05 – 0.10	**<0.001**
Phenotype [selfish]	2.22	1.78 – 2.77	**<0.001**	1.22	0.89 – 1.68	0.216
Frequency of altruists [linear]	21.58	11.79 – 39.49	**<0.001**	7.79	3.74 – 16.24	**<0.001**
Frequency of altruists [quadratic]	0.73	0.45 – 1.18	0.194	1.18	0.72 – 1.94	0.507
Frequency of altruists [cubic]	0.71	0.48 – 1.04	0.075	0.68	0.46 – 1.00	**0.048**
Number of injuries incurred				0.12	0.09 – 0.15	**<0.001**
Resources acquired by focal prey				3.47	2.97 – 4.05	**<0.001**
Number of times the focal prey got rescued				2.73	2.22 – 3.36	**<0.001**
Number of times the focal prey recued another prey				0.64	0.50 – 0.82	**<0.001**
Number of times all prey got injured by the predator				0.51	0.40 – 0.65	**<0.001**
Resources acquired by rescued prey				1.30	1.09 – 1.54	**0.004**
Duration as maximum group size (4 prey)				5.64	4.46 – 7.14	**<0.001**

Random Effects

σ^2	3.29	3.29
τ_{00}	4.58 $_{\text{match\_id}}$	3.38 $_{\text{match\_id}}$
	0.25 $_{\text{mirrors\_id}}$	0.35 $_{\text{mirrors\_id}}$
	1.62 $_{\text{killer\_id}}$	1.04 $_{\text{killer\_id}}$
ICC	0.66	0.59
N	1388 $_{\text{match\_id}}$	1388 $_{\text{match\_id}}$
Observations	5552	5552
Marginal R^2 / Conditional R^2	0.089 / 0.692	0.572 / 0.825

The full model identified the following relationships. The number of predator-related injuries incurred by focal prey (odds ratio = 0.12, CI = 0.09 – 0.15, p < 0.001, Table 3) and by the whole group (odds ratio = 0.51, CI = 0.40 – 0.65, p < 0.001, Table 3) both decreased survival. In line with our prediction, rescuing a group member decreased the altruist’s survival probability (odds ratio= 0.64, CI=0.50 – 0.82, p <0.001, Table 3). The number of times that the focal prey was rescued from capture significantly increased its survival as well (odds ratio= 2.73, CI=2.22 – 3.36, p <0.001, Table 3) and the number of resources acquired by rescued prey increased the survival of altruistic individuals (odds ratio = 1.30, CI = 1.09 – 1.54, p = 0. 004, Table 3), as expected. In line with our prediction, prey survival was largely and positively affected by the time that the group comprised four members (odds ratio = 5.64, CI = 4.46 – 7.14, p < 0.001, Table 3). Survival also increased with the amount of resources acquired by the focal prey (odds ratio= 3.47, CI=2.97 – 4.05, p <0.001, Table 3).

APPENDICE F

Full model A

Table 4.2 Parameters and results for full Model A including the types of character chosen by the prey and the type of virtual environment in which the trial takes place. Estimates for fixed effect are odds ratios with 95% confidence intervals (CI) in parentheses. *p < 0.05. *** p < 0.001. The sample size is n = 16,272.

Interpretation	Variables	Model A
Fixed effect	Total number of injuries	1.50 (1.48 – 1.53) ***
Random effect	Focal prey ID	0.0706
	ID of the virtual environment (random effect)	0.0000
	ID of the character of the prey (random effect)	0.0004
	ID of the item of the prey (random effect)	0.0002
	Marginal R^2	0.187
	Akaike information criterion	41890

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