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Tracey Hammer

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Anti-predator behaviors: Sources of variation and reproductive consequences

PhD ADVISORS:

Dr. Jean Patrice ROBIN	Director of research, IPHC, UMR 7178, CNRS, Strasbourg
Dr. Pierre Bize	Director of research, Vogelwarte, Sempach, Switzerland

External REFEREE:

Dr. François-Xavier Dechaume-Moncharmont	Professor, LEHNA, UMR 5023, CNRS, Lyon
Dr. Ursula Ellenberg	Lecturer, University of Otago, Dunedin

Internal REFEREE:

Dr. Sylvie Massemin	Professor, IPHC, UMR 7178, CNRS, Strasbourg

---

GUEST:

Dr. Vincent Viblanc	Researcher, IPHC, UMR 7178, CNRS, Strasbourg

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THÈSE

Présentée par :

Tracey Hammer

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Comportements anti-prédateurs : Sources de variations et Consequences reproductives

THÈSE dirigée par :	
Dr. Jean Patrice ROBIN	Directeur de recherche, IPHC, UMR 7178, CNRS, Strasbourg
Dr. Pierre Bize	Directeur de recherche, Volgelwarte, Sempach, Switzerland
RAPPORTEURS externes :	
Dr. François-Xavier Dechaumes-Moncharmont	Professeur, LEHNA, UMR 5023, CNRS, Lyon
Dr. Ursula Ellenberg	Maître de conférences, Université d'Otago, Dunedin
RAPPORTEUR interne :	
Dr. Sylvie Massemin	Maître de conférences, IPHC, UMR 7178, CNRS, Strasbourg
INVITÉ :	
Dr. Vincent Viblanc	Chargé de recherche, IPHC, UMR 7178, CNRS, Strasbourg

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DEDICATION

To Myrna Hammer,

a mother in absentee,

missed but not forgotten

Papers presented in this thesis:

1. **Hammer, TL,** Bize, P, Saraux, C, Gineste, B, Robin, J-P, Groscolas, R, and Viblanc, VA. 2022. Repeatability of alert and flight initiation distances in king penguins: effects of colony, approach speed and weather. Ethology, 128, 303– 316. https://doi.org/10.1111/eth.13264
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Communications:

1. **Hammer, TL,** Viblanc, VA, Stier, A, Michaux, D, Voisin, E, Robin, J-P, Bize, P, and Schull, Q. 2019. Does auricular patch size act as a status signal in king penguins? *10th International Penguin Conference*, Dunedin, New Zealand.
2. **Hammer, TL,** Viblanc, VA, Stier, A, Michaux, D, Voisin, E, Robin, J-P, Bize, P, and Schull, Q. 2019. Does auricular patch size act as a status signal in king penguins? *EPE meeting*, Strasbourg, France.

3. **Hammer, TL,** Bize, P, Saraux, C, Gineste, B, Robin, J-P, Groscolas, R, and Viblanc, VA. 2021. Repeatability of alert and flight initiation distances in king penguins: effects of colony, approach speed and weather. *AVEC meeting,* Strasbourg, France.
4. **Hammer, TL,** Bize, P, Saraux, C, Gineste, B, Robin, J-P, Groscolas, R, and Viblanc, VA. 2021. Repeatability of alert and flight initiation distances in king penguins: effects of colony, approach speed and weather. *Bize lab group*, Aberdeen, Scotland.
5. Lewden, A, Ward, C, Avril, S, Abolivier, L, Gérard, C, **Hammer**, **TL,** Robin, J-P, Viblanc, VA, Bize, P, and Stier, A. 2022. Surface temperatures are influenced by handling stress independently of glucocorticoid levels in wild king penguins. *18 JS du CNFRA*, Toulouse, France.

ABSTRACT

Coping with the threat of predation is a central aspect of the life of many animal species. In order to avoid predators, a first line of defense is to use vigilance behavior; in other words, the active scanning of the environment for potential threats. Once a predator is detected, prey use a variety of strategies to avoid predation. Although many anti-predation strategies have evolved (for example, the use of crypsis and refuges, physical defenses and toxins, and group mobbing), almost all species will utilize basic flight behavior in an attempt to avoid predation. When a threat is detected (the distance at which an approaching predator is detected is called the Alert Distance, AD), at some point, the predator will approach too near for comfort and flight behavior away from the threat will be initiated. The distance to which a predator can approach a prey before flight is initiated is termed the Flight Initiation Distance, or FID. Finally, once flight has been initiated, the prey will flee for some maximal distance away from the predator before stopping, termed the Distance Fled, DF.

The exact distance at which a prey decides to initiate flight from a predator (i.e., FID) is thought to be determined by a risk assessment undertaken by the prey. Escape theory proposes that FID will be longer when prey evaluate predator approaches as highly risky in terms of injuries or survival, for example if they are being approached by many predators, approached directly, or approached rapidly (as when the predator displays increased intent of attack). It also suggests that FID may be shortened if the site that the prey is utilizing has advantages that the prey does not want to lose by initiating flight, for example, a site with high forage potential. The end result of this risk assessment according to escape theory is that prey should initiate flight only when the benefits of staying equal the costs of leaving; however, an additional theory called “optimal escape theory” has further expanded the idea by saying prey may conduct activities that enhance fitness more than the cost incurred during a predation encounter. This could occur when the prey is courting mates, defending a territory or protecting offspring, if such activities end up in net fitness benefits that outweigh the fitness costs associated with potential injury or decreased survival. Although antipredator behaviors are fairly well researched in a variety of angles (in particular FID, but much less so for AD and DF), fairly little is known on how those are shaped by life history traits, environmental variation and the value of reproduction in colonial seabirds. This thesis explores how AD, FID and DF, in colonial king penguin (*Aptenodytes patagonicus*) are shaped by their biotic and abiotic environment, their life history characteristics, and the value of reproduction.

King penguins are flightless seabirds that molt and breed on islands throughout the sub-Antarctic regions of the Southern Ocean. On land, and particularly during breeding, they form massive colonies

containing tens of thousands of individuals. In those colonies, penguins are subject to on-land predation by giant petrels and sub-Antarctic skuas that mostly target eggs and chicks, but occasionally also predate adults. Breeding individuals fiercely defend small reproductive territories against aggressive conspecifics and predators. Because breeding adults incubate and raise a single egg/chick per breeding season on their feet, and because these seabirds are flightless, adults must make decisions on how closely they let predators approach before initiating flight and abandoning reproduction altogether. Breeding king penguins can be followed over several months, allowing for repeated approaches to be performed on the same individuals. King penguins have a highly demanding reproductive cycle which takes up to 14-16 months to complete. The single chick produced per reproductive attempt requires cooperation between both partners (alternating between parental care on-land and foraging at sea) to fledge successfully. If the attempt to breed fails early, re-nesting potential is low, as late breeding partners almost never are successfully able to fledge a chick. This model system thus provides the perfect opportunity to study how AD, FID, an DF vary in response to fitness trade-offs shaped by predation risk and breeding activities in a prey species that is highly constrained by reproductive demands. This model system enables us to test many hypotheses simultaneously (such as different but mutually non-exclusive hypotheses regarding social grouping), to compare different life history stages, something which has not been previously done, and to compare costs and benefits to living on the outskirts of a social grouping. In the following studies, we used non-lethal approaches performed by a human as a model to simulate approaches by an actual predator. Human approaches make for good simulations because animals are selected overestimate rather than underestimate risk, and both types of approaches result in the same decision-making processes in the target animal, since both divert time and energy that could otherwise be invested in fitness enhancing activities.

Chapter 1 quantifies the variability of antipredator behaviors in king penguins through several questions. First, I question whether AD, FID, and the decision to flee, varies between two colonies of king penguins with different exposure to human disturbance. Studies suggest that animals may acclimatize to human presence over time as animals realize that humans rarely pose a significant threat. This means that prey animals tend to allow humans to approach closer, resulting in shorter FID. Yet, there remains the chance that animals may find humans unpredictable and risky, resulting in sensitization and increased FID and flightiness. Second, I asked whether AD, FID, and the decision to flee were repeatable behavioral traits. If these behaviors are repeatable, they can be considered as personality traits. Finally, I considered whether additional factors such as the weather, time of day, and approach speed affected antipredator behaviors. Over three consecutive days, a single experimenter approached 47 incubating king penguins in two different colonies that varied in their level of human disturbance. In one colony, penguins see humans on almost a daily basis, while in the other colony, humans visit only once or twice a year for population surveys. One of the first results to stand out is that incubating king penguins do not always choose to initiate flight from an approaching human (12.8% of approached resulted in an FID of 0). FID and the decision to flee were moderately repeatable (r=0.26 and 0.57, respectively). As is common to see in studies of FID, FID increased with increasing approach speed, suggesting an evaluation of risk by the animals. Weather had an effect on all three antipredator behaviors: AD increased in warm sunny weather, and in rainy, windy weather birds were more likely to flee but waited longer before initiating flight. There was no evidence of habituation or sensitization in either colony, neither in the short span of three days, or in long term differences between the colonies.

In Chapter 2, I explored the effect of group living and social distractions on anti-predator behaviors (AD, FID, and the decision to flee) by testing four different hypotheses. The presence of many individuals could increase the ability of the group as a whole to detect an approaching threat ("many-eyes" hypothesis); the presence of many individuals also lowers predation risk to each individual assuming the predator can take only one prey at a time ("dilution effect" hypothesis). Individuals in the center of the colony may have relative safety if the prey on the edge of the colony are more vulnerable ("selfish herd" hypotheses), but yet, the increased number of social cues emitted by neighbors may distract from detecting predators ("distracted prey" hypothesis). These hypotheses all predict different effects on AD and FID with increasing group size or density: the many-eyes hypothesis predicts increased ADs, the dilution effect predicts reduced FIDs, the selfish herd predicts reduced FIDs in the center of the colony), and the distracted prey hypothesis predicts reduced AD and FID, and increased likelihood to not initiate flight. During reproduction, king penguins form massive colonies, and the presence of other individuals could potentially assist or hinder predator detection and avoidance. For example, penguins in the center of the colony could be relatively safer, and yet high levels of territorial aggression may hinder the ability of an individual to detect the approach of a threat. We approached 200 incubating king penguins at different points in the breeding season when overall colony density was low, medium, high, or maximal. To test the "many-eyes" and "dilution effect hypotheses", we measured relative local neighbor density. We also measured rank in the colony from edge to center to test the "selfish herd" hypothesis, and to test the "distracted prey" hypothesis we also measured the number of aggressions the focal bird emitted towards neighbors during the approach. Thanks to our model system, this is the first study of its kind to simultaneously study all four of these hypotheses. We found that birds engaged in aggressive conflicts with neighbors were less likely to flee, and that increasing relative local neighbor density at low and medium overall colony densities resulted in a decrease in bird AD, both supporting the “distracted prey” hypothesis. Yet, at maximal overall colony density, increasing relative local neighbor density resulted in longer AD, supported the “many-eyes” hypothesis. We found no effects with FID, and also no support for the “dilution effect” or the “selfish herd” hypothesis in this study.

In Chapter 3, I compared antipredator behavioral responses (in terms of AD, FID, the decision to flee or not, and DF) between different life history stages (molting birds, birds not engaged in reproductive activities, courting birds, birds in breeding pairs, incubators, birds brooding young, thermally dependent chicks, and birds brooding older thermally independent chicks). This provided the chance to explore optimal escape decisions with regards to the various life history stages of the breeding cycle, where the associated costs of fleeing were expected to differ. For example, by fleeing courting birds risk losing the partner they’ve been wooing, breeding birds risk losing their mate and territory, incubators risk losing their egg, etc. I also tested the “brood value hypothesis” which predicts increasing parental investment as the offspring ages due to increasing probability of surviving to adulthood. In terms of our experiment, this means that chicks are of higher value than eggs, and therefore the parent should invest more into offspring defense and be less willing to flee upon the approach of a threat when they have a chick over an egg. Finally, I similarly tested reproductive value and parental investment by comparing early and late breeders. Since late breeders have practically no chance of successfully fledging a chick, they should invest less into offspring defense, be more likely to flee, and flee sooner than early breeding birds. We approached a total of 567 individuals, 467 were compared according to life history stage, and the final 100 were used to compare early and late breeders. We found that molting birds and non-reproductive birds had significantly higher AD than the other life history stages, possibly because they have the least social distractions (see Chapter 2). The life history stages longest FID and DF were molting birds and non-reproductive birds, suggesting they had either the lowest costs of flight or the lowest site fidelity. The life history stages with the highest cost of flight were breeding birds and incubators and brooders of young chicks, as they had the shortest FID and DF. As for the brood value hypothesis, king penguins followed the expected results for an animal with semi-altricial offspring. Parental investment in offspring defense did not change greatly between incubation and brooding young thermally dependent chicks (incubators and brooders of young chicks were equally likely to flee, and had similar DF, although incubators had significantly shorter FID), but parental investment was reduced once the chicks had aged and gained independent movement (i.e., when they were older and thermally independent). Brooders of older chicks were significantly less aggressive, chose to flee significantly more often, and had longer DF than brooders of young, dependent chicks. Incubating birds and brooders of young chicks were the most aggressively defensive life history stages, while all others chose to flee instead of stay and aggressively fight the approaching threat. Finally, late breeders were significantly more likely to initiate flight than early breeders, suggesting reduced investment in their offspring, however their AD, FID and DF were comparable to early breeding birds.

Overall the results stemming from this PhD thesis shows that, in king penguins, antipredator behaviors are determined both by environmental factors (weather), potential threat in the approach (approach speed), social environment (including social distraction), cost of flight (reproductive investment), and individual characteristics (personality). Interestingly, breeding king penguins, similar to other ground-nesting birds, may regularly choose not to flee from an approaching threat and instead stay and defend their young aggressively, a characteristic that is not seen when king penguins are in non-reproductive life history stages. These results show that behavioral decisions towards approaching threats are complex and likely explained by a range of mutually non-exclusive hypotheses. Thanks to the advantages of this animal model (colonial, aggressive, ground nesting, ability to follow individuals, presence of multiple life history stages), I had the unique opportunity to test many currently existing hypotheses (for example, the social grouping hypotheses, or the brood value hypothesis) together in one species, something that is rarely possible.

RÉSUMÈ de la thèse

Faire face à la menace de la prédation est un aspect central de la vie de nombreuses espèces animales. Afin d'éviter les prédateurs, une première ligne de défense est souvent l'utilisation d'un comportement de vigilance ; en d'autres termes, l'analyse active de l'environnement à la recherche de menaces potentielles. Une fois qu'un prédateur est détecté, la proie utilise une variété de stratégies pour éviter la prédation. Bien que de nombreuses stratégies anti-prédation aient évolué (utilisation d'abris ou de refuges, défenses physiques et toxines, coopération et harcèlement de groupe), presque toutes les espèces ont recours au comportement de fuite pour éviter la prédation. Lorsqu'une menace est détectée, une proie potentielle initiera un comportement de fuite dès lors que le prédateur s'approchera trop près de celle-ci.

Cette distance minimale, appelée distance de fuite ou FID, est déterminée par une évaluation du risque encouru par la proie. La théorie de l'évasion optimale propose que cette FID soit plus longue lorsque le risque de prédation réel augmente, par exemple si l'individu est approché rapidement ou en trajectoire directe par un prédateur (signalisant une intention accrue du prédateur), ou encore par de nombreux prédateurs, plutôt qu'un prédateur isolé. Au contraire, cette distance peut être raccourcie si le site/l'habitat sur lequel/laquelle se trouve la proie présente des avantages qui seraient perdus en initiant le fuite, par exemple, un site d'intérêt alimentaire ou favorable à la reproduction, par exemple lorsque la proie courtise des partenaires sexuels, défend un territoire ou protège sa progéniture. Le résultat final de cette évaluation des risques est que les proies ne devraient initier la fuite que lorsque les avantages l'emportent sur les coûts en termes de valeur sélective (survie et reproduction). Bien que les comportements anti-prédateur soient bien étudiés, relativement peu est connu sur comment ces comportements sont façonnés par les traits d'histoire de vie, la variabilité environnementale et la valeur de la reproduction chez les oiseaux marins.

Cette thèse explore les facteurs extrinsèques et intrinsèques ayant façonné le comportement anti-prédateurs chez un oiseau marin colonial, le manchot royal (*Aptenodytes patagonicus*). Ces comportements de réponse à l'approche d'un prédateur incluent la distance de alerte (AD) égale à la distance proie-prédateur à laquelle un prédateur est détecté, la distance de fuite (FID) égale à la distance proie-prédateur à laquelle la proie initie un comportement de fuite, et la distance fuite (DF) correspondant à distance maximale sur laquelle une proie fuit une fois la fuite initiée.

Les manchots royaux sont des oiseaux marins se reproduisant sur les îles des régions subantarctiques de l'océan Austral. Sur terre, et particulièrement lors de la reproduction, ils forment de larges colonies contenant des dizaines de milliers d'individus. Dans ces colonies, les manchots sont soumis à des prédateurs terrestres (pétrels géants et skuas subantarctiques) qui ciblent principalement les œufs et les poussins, mais parfois aussi les adultes. Les individus reproducteurs défendent farouchement de petits territoires de reproduction contre ces prédateurs mais également contre leurs congénères. Lorsqu'ils sont menacés par des prédateurs, les adultes sont confrontés à un choix : rester pour protéger leur progéniture (œuf ou jeune poussin non émancipé, *c-à-d* leur investissement reproductif) au détriment potentiel de leur survie, ou fuir et abandonner la reproduction en cours. Ce choix est façonné par la valeur sélective relative de chaque stratégie. Le manchot royal a un cycle de reproduction long qui s’étend sur 14 à 16 mois, jusqu’à l’indépendance du poussin. Au maximum un seul poussin est produit à chaque cycle reproducteur, et il est rare qu’un adulte réussisse deux reproductions successives. Par ailleurs, la reproduction nécessite une coopération étroite entre les deux partenaires (alternant entre soins parentaux à terre et recherche alimentaire en mer) pour réussir. Si la tentative de reproduction échoue, le potentiel de re-nidification est faible. Ces animaux constituent ainsi un modèle d’étude intéressant pour comprendre comment les comportements anti-prédateurs (distances AD, FID et DF) sont sélectionnées au regard du compromis évolutif existant entre reproduction et survie. Par ailleurs, le comportement territorial et l'agressivité élevée entre congénères voisins est également susceptible de façonner ces comportements anti-prédateurs. L’agressivité entre congénères est une cause de distraction potentielle quant à la vigilance envers les prédateurs, offrant une opportunité de tester les coûts potentiels de la vie en colonie. Finalement, les manchots royaux peuvent être suivis sur plusieurs mois, permettant d'effectuer des approches répétées sur les mêmes individus, et d’évaluer l’aspect plastique ou non des réponses anti-prédateurs.

Au cours de cette thèse, j’ai utilisé chez les manchots royaux des approches non létales effectuées par un humain pour simuler des approches d'un prédateur réel. Les approches humaines non-léthales ont été démontrées comme étant une méthode fiable pour évaluer les réponses anti-prédatrices, car 1) elles entraînent les mêmes processus de prise de décision chez l'animal que des approches de prédateur réel (les deux détournent du temps et de l'énergie autrement investis dans des activités de maintenance ou de reproduction) et car 2) les animaux sont sélectionnés pour surestimer plutôt que pour sous-estimer le risque de prédation.

Dans le 1^{er} chapitre de cette thèse, j'ai exploré la variabilité du comportement anti-prédateur chez le manchot royal. Premièrement, j'ai testé si les comportement anti-prédateurs (AD, FID et la décision de fuir) variaient entre deux colonies de manchots royaux soumises de manière chronique à différentes perturbations anthropiques. Plusieurs études suggèrent en effet que des animaux exposés continuellement à l'homme peuvent s'habituer à sa présence au cours du temps, tolérant des approches humaines plus proches lors d'approches répétées. Cependant des résultats contradictoires ont également été obtenus, avec une sensibilisation des animaux aux approches humaines répétées et une augmentation de la FID et de la DF. Deuxièmement, j'ai testé si AD, FID et la décision de fuir sont des traits comportementaux répétables. Si ces comportements sont répétables, ils peuvent être considérés comme des traits de personnalité. Finalement, j'ai examiné si des facteurs environnementaux tels que les conditions météorologiques, l'heure de la journée et la vitesse d'approche affectent les comportements anti-prédateurs. Pendant trois jours consécutifs, 47 manchots royaux en incubation ont été approchés dans deux colonies différentes soumises à différents niveaux de dérangement anthropique. L'un des premiers résultats marquant est que les manchots royaux en incubation ne choisissent pas toujours de fuir à l'approche d'un humain (c. a. 13% des oiseaux avaient un FID égal à 0). La FID et la décision de fuir étaient modérément répétables (r = 0,26 et 0,57, respectivement). La FID augmente avec l'augmentation de la vitesse d'approche, ce qui suggère une évaluation du risque par les animaux. Les conditions météorologiques ont eu un effet sur les trois comportements anti-prédateurs : l'AD était augmentée par temps chaud et ensoleillé, et par temps pluvieux et venteux, les oiseaux étaient plus susceptibles de fuir, mais ont attendu plus longtemps avant de fuir. Nous n'avons pas mis en évidence d'effet d'habituation à court-terme ou sensibilisation dans l'une ou l'autre des colonies au cours du temps.

Dans le 2nd chapitre de cette thèse, j'ai exploré l'effet de la vie en groupe et des distractions sociales liée à l'agressivité coloniale sur les comportements anti-prédateurs (AD, FID et décision de fuir) en testant quatre hypothèses différentes. J'ai testé plusieurs hypothèses évolutives, non-mutuellement exclusives, ce qui est rarement réalisé conjointement chez l'animal sauvage. La présence de nombreux individus pourrait augmenter la capacité du groupe dans son ensemble à détecter une menace qui approche (hypothèse « des yeux multiples ») ; la présence de nombreux individus réduit également le risque de prédation pour chaque individu sous l'hypothèse que le prédateur ne peut prédater qu'un seul individu à la fois (hypothèse « de dilution »). Par ailleurs, les individus au centre du groupe (ou de la colonie) devraient également avoir un risque de prédation plus faible que ceux en périphérie (hypothèse du « troupeau égoïste »). Toutefois, un nombre accru de perturbations sociales émises par des voisins devraient détourner l'attention de proies potentielles de la détection de prédateurs (hypothèse de « la proie distraite »). Ces hypothèses prédisent toutes des effets différents sur AD et FID avec l'augmentation de la taille ou de la densité du groupe : l'hypothèse des yeux multiples yeux prédit une augmentation d'AD, l'effet de dilution prédit une réduction de FID, le troupeau égoïste prédit une réduction de FID au centre de la colonie, et l'hypothèse de la proie distraite prédit une réduction d'AD et de FID ainsi qu'une probabilité accrue de ne pas initier de fuite. Pendant la reproduction, les manchots royaux forment des colonies importantes et denses et la présence d'autres individus pourrait avoir des effets antagonistes, soit positifs soit négatifs, sur la détection et l'évitement des prédateurs. Par exemple, les manchots au centre de la colonie pourraient être relativement plus sûrs, et pourtant des niveaux élevés d'agression territoriale peuvent entraver la capacité d'un individu à détecter l'approche d'une menace. Nous avons approché 200 manchots royaux en incubation à différents moments de la saison de reproduction lorsque la densité globale de la colonie était faible, moyenne, élevée ou maximale. Pour tester les hypothèses « yeux multiples » et « effet de dilution », nous avons mesuré la densité locale relative des voisins de l'animal testé. Nous avons également mesuré le rang des reproducteurs testés dans la colonie du bord vers le centre pour évaluer l'hypothèse du « troupeau égoïste ». Pour tester l'hypothèse de la « proie distraite », nous avons mesuré le nombre d'agressions émises par l'oiseau étudié envers ses voisins lors de l'approche par l'expérimentateur. Nos résultats montrent que 1) les oiseaux impliqués dans des conflits agressifs avec leurs voisins étaient moins susceptibles de fuir et 2) que l'augmentation de la densité relative des voisins locaux à des densités globales de colonies faibles et moyennes entraînait une diminution de l'AD des oiseaux, supportant ainsi l'hypothèse de la « proie distraite ». Pourtant, quand la densité globale des colonies est maximale, l'augmentation de la densité relative des voisins locaux a entraîné une AD plus importante, confirmant l'hypothèse des « yeux multiples ». Nous n'avons trouvé aucun effet sur FID, et également aucun support pour les hypothèses de « l'effet de dilution » ou du « troupeau égoïste » dans cette étude.

Dans le 3^{e} chapitre de cette thèse, j'ai comparé les réponses comportementales anti-prédatrices des oiseaux (en termes de AD, FID, la décision de fuir ou non et DF) entre différents stades d'histoire de vie (oiseaux en mue, non engagés dans des activités de reproduction, en parade, en couples territoriaux, oiseaux sur œuf, sur jeunes poussins thermiquement dépendants, et sur poussins plus âgés et thermiquement indépendants). Cette étude a permis d'explorer chez les manchots royaux comment les réponses anti-prédatrices sont sélectionnées en fonction des phases du cycle de vie et du cycle de reproduction, pour lesquels les coûts/bénéfices associés à la fuite en termes de valeur sélective devaient différer. Par exemple, pendant la reproduction, la fuite est associée au risque d'abandon (perte du partenaire, du territoire, de l'œuf ou du poussin). Par ailleurs, chez cette espèce, la reproduction peut être initiée sur une période assez longue de 5 mois, entre novembre et mars et les reproducteurs sont qualifiés de précoces ou tardifs selon leur date de mise en couple ; le succès reproducteur étant d'autant plus faible que la date de début de cycle est tardive. J'ai donc également testé la valeur reproductive et l'investissement parental en comparant des reproducteurs précoces et tardifs. Étant donné que ces derniers ont un faible succès de reproduction, ils devraient moins investir dans la défense de la progéniture et être plus susceptibles de fuir à l'approche d'un prédateur que des oiseaux reproducteurs précoces. Au cours de cette étude, nous avons approché un total de 567 individus, dont 467 ont été comparés selon leur stade d'histoire de vie, et 100 ont été utilisés pour une comparaison reproducteurs précoces *vs* tardifs. Les résultats montrent que des oiseaux en mue et des oiseaux non reproducteurs avaient une AD significativement plus élevée que lors des autres stades d'histoire de vie, probablement car moins soumis aux distractions sociales (voir chapitre 2). Les oiseaux en mue et non reproducteurs, avaient par ailleurs les FID et DF les plus élevés, car non contraints par la reproduction. Les stades les moins susceptibles de fuir étaient les couples territoriaux > oiseau couvant un œuf > parents de jeunes poussins. Nos résultats obtenus chez les manchots royaux sont ainsi conformes à ceux attendus chez un animal semi-nidicole. L'investissement parental est similaire pour des parents couvant des œufs ou gardant de jeunes poussins thermiquement, mais est réduit une fois que les poussins ont atteint un âge plus avancé et sont thermiquement indépendants. Les oiseaux couvant un œuf et les parents de jeunes poussins étaient les plus agressifs, tandis que pour tous les autres stades d'histoire de vie ils ont plutôt tendance à fuir à l'approche d'un prédateur. Les parents de poussins plus âgés étaient significativement moins agressifs, initiaient plus fréquemment un comportement de fuite, et avaient une DF plus longue que les parents de jeunes poussins. Enfin, les reproducteurs tardifs étaient significativement plus susceptibles de fuir que des reproducteurs précoces, suggérant un investissement parental réduit, bien que les AD, FID et DF étaient comparables entre ces deux groupes.

En conclusion, les résultats issus de cette thèse de doctorat montrent que chez les manchots royaux, les comportements anti-prédateurs sont déterminés à la fois par des facteurs environnementaux (météorologiques), l'évaluation de la menace potentielle de prédation (vitesse d'approche), l'environnement social (y compris distractions sociales), le coût de la fuite en termes de valeur sélective (reproduction investissement), et des caractéristiques individuelles propres aux oiseaux (personnalité). Les manchots royaux, comme d'autres oiseaux nichant au sol, peuvent régulièrement choisir de ne pas fuir une menace imminente et de rester défendre leur poussin de manière agressive, une caractéristique non-observée chez des oiseaux non reproducteurs. Ces résultats montrent que les décisions comportementales à l'égard des menaces à l'approche sont complexes et probablement expliquées par une série d'hypothèses mutuellement non exclusives.

ABBREVIATIONS

AD	Alert Distance
FID	Flight Initiation Distance
DF	Distance Fled
BDM	Baie du Marin
JJ	Jardin Japonais

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INTRODUCTION

1. Predation as a central selective agent on population size, dynamics, and ecosystem function

Predation, the act in which predators capture prey and ingest them for nutrients and energy, has major consequences on the natural population sizes and dynamics of both the prey and predator, often shaping the functioning of entire ecosystems. A classic example of predation acting on the population size and dynamics of both the predator and prey are the cyclical population trends seen between snowshoe hare, *Lepus americanus*, and lynx, *Lynx canadensis* (Keith 1962, Krebs et al. 2001, Nellis et al. 2009) (Fig 1a). Not only are the populations of snowshoe hare and lynx involved in this cycle, but many populations of other species which share the same ecosystem are also implicated (Boutin et al. 1995). Similar interdependent populations trends can be seen between moose (*Alces alces*) and wolves (*Canis lupus*) on Isle Royale (Mech 1966, Peterson et al. 1998) (Fig 1b). Isle Royale was originally colonized by moose early in the 1900s and remained that way until a small population of wolves crossed an ice bridge to the island in the late 1940s (Peterson 1999). When wolf population declined in the 1980s (most likely due to disease and inbreeding), moose populations skyrocketed, leading to a record high of 2400 individuals by 1996 before collapsing to 500 moose due to a severe lack of forage, disease, and harsh winter (Peterson 1999). We can see from this last example that predators not only affect population size and dynamics, but also ecosystem functioning as well through trophic cascades (see also Boutin et al. 1995, and references within). By limiting the number and altering the behavior of herbivores through predation, vegetation is able to flourish. Reintroduction of wolves to Yellowstone National Park in 1995 has led to a lowering of elk (*Cervus elaphus*) population size and foraging pressure, causing an increase in riparian diversity and biomass (Beschta and Ripple 2016). In another ecosystem, seabird colonies enhance nutrient provisioning to coral reefs in coastal areas, thus increasing fish biomass, yet the introduction of rats (which predate eggs and young chicks) to many islands have decimated breeding colonies and impacted cross-ecosystem nutrients flows (Benkwitt et al. 2022). Species lower in the trophic chain (insects, rodents, herbivorous species) face the highest predation pressure (Sinclair et al. 2003, Faithfull et al. 2011, Papacostas and Freestone 2019), however, even predators themselves can occasionally suffer from predation, particularly their young. Giant petrels (*Macronectes* spp.), while being top predators, face predation of their eggs and chicks by invasive rat and cats (Phillips et al. 2016). In fact, in many species (particularly long-lived species), offspring (eggs, larva, chicks, young) face the most dramatic predation risk (Rodd and Reznick 1997, Fontaine and Martin 2006, Martin and Briskie 2009). Given the far-reaching consequences of predation, predator-prey interactions can provide important insights on ecosystem functioning and trophic interactions.

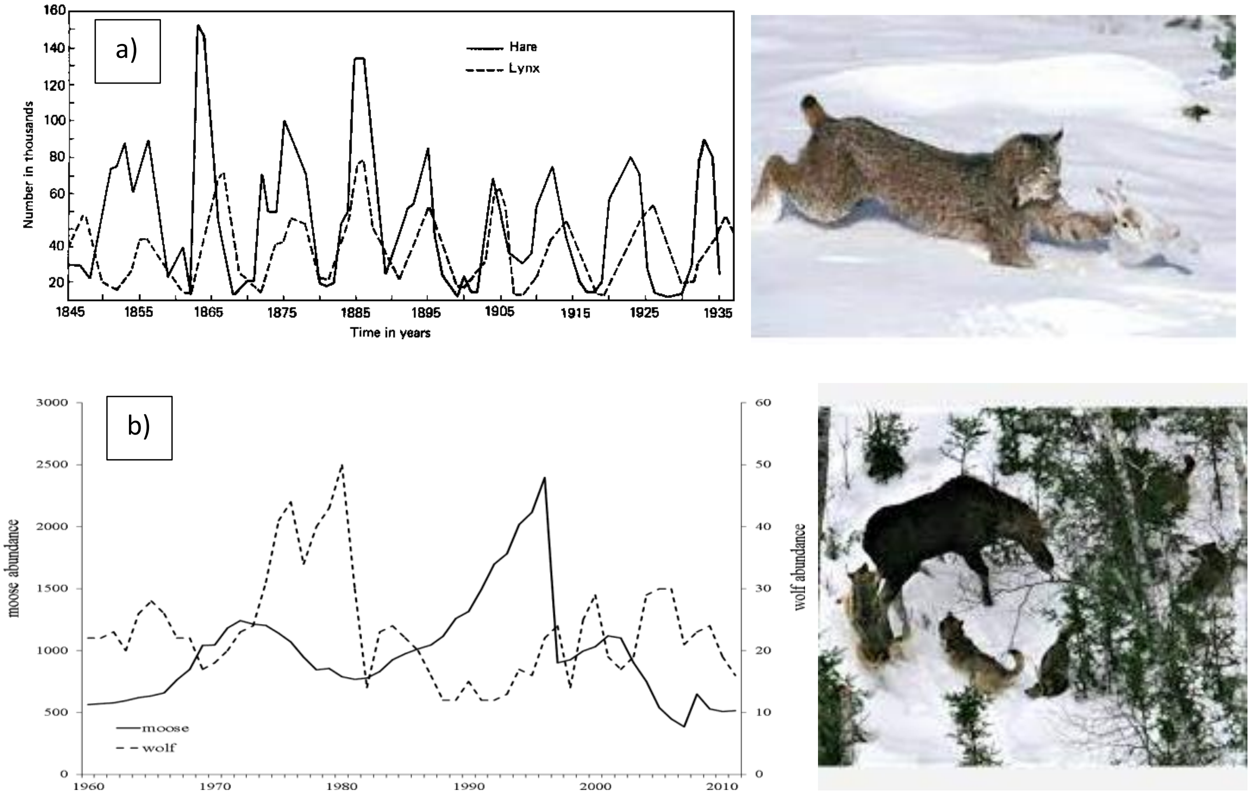


Figure 1. Population interdependency of predators and prey. a) Population cycling of snowshoe hare (*Lepus americanus*) and lynx (*Lynx canadensis*). Reproduced from MacLulich 1937. b). Population cycles of moose (*Alces alces*) and the wolves (*Canis lupus*) on Isle Royale. Reproduced from Sattler et al. 2017.

2. Antipredator behaviors and their evolution

Not only can the act of predation lead to an abrupt end in prey future fitness, predation attempts obviously incurring direct costs through lethality, yet predation also incurs indirect costs to the prey, either through increased stress (Clinchy et al. 2004, Sheriff et al. 2009, 2011) with sometimes long-term consequences on future generations (Sheriff et al. 2010, 2015), or because prey attempts to avoid predation imply necessary changes in behavioral time-budgets and associated energy usage when attempting to flee the predator (Sheriff et al. 2009, McCauley et al. 2011). Even predation pressure alone, or the risk of potential predation, can interrupt or alter ongoing beneficial activities for the prey, such as the interruption of foraging (resulting in a loss of nutrient and energy uptake, Wirsing et al. 2008), resting, or breeding activities (mate choices, offspring care, or territory defense, Cooper and Blumstein 2015), and cause physiological changes such as increased stress levels in the prey (Sheriff et al. 2009, 2011, Hawlena and Schmitz 2010). For example, foraging marine mammals (dolphins, *Tursiops* sp., harbor seals, *Phoca vitulina*, and dugongs, *Dugong dugon*) avoid spending time in more profitable, but more dangerous, patches when predation risk is high (Wirsing et al. 2008). Due to these costs, there should be strong selection on species to evolve morphological, physiological, behavioral or life history strategies to deal with the risk of predation. The evolution of those strategies should depend on the trophic level of the considered species, with stronger selection acting on species lower in the food web. In order to avoid predation, prey have evolved various strategies, which will be discussed below, including the use of flight behavior, crypsis, refuges, physical or physiological defenses such as spines, armor, or toxins, or the use of autotomy of limbs and tails.

3. Types of antipredator responses

3.1 Morphological adaptations: defenses, armaments, mimicry, and autotomy

In an attempt to prevent predation, animals have evolved morphological adaptations that increase the difficulty of a predation attempt or increase the risk of injury and death to the attacking predator. Examples of increasing the difficulty of predation include hardened exoskeletons seen in insects and crustaceans (Barshaw et al. 2003, Tarsitano et al. 2006, Wang et al. 2018). Fish can also possess armor and spines to impede the ease of predation; brook stickleback (*Culea inconstans*) is one of these (Abrahams 1995), as can mammals although rarely (armadillo, *Cingulata* sp., Superina and Loughry 2012). Spines are a common adaptation that risks injury to the potential predator, and is seen in insects, crustaceans, and fish (Feifarek 1987, Meuthen et al. 2018, Sugiura 2020), yet the classical example is the mammalian porcupine (for example Mori et al. 2014). Prey may also possess weapons, such as pincers in crabs and lobsters (Barshaw et al. 2003), and horns/antlers in mammals (Packer 1983, Stankowich and Caro 2009). Even morphological changes to colors or patterns aid in reducing the threat of predation. Conspicuous “eye spots” that are found in fish and lepidopterans serve to startle and intimidate the predator, leading to a reduced number of predation attempts (Stevens et al. 2008). Some changes in color and shape have gone so far as to mimic other species that are less desirable to ingest; spider mimicking moths (*Brenthia coronigera*) even move and behave in such a way to pull off this deception (Wang et al. 2017). A final type of morphological defense is autotomy, or the purposeful casting off of a limb or appendage when under threat, allowing the targeted prey to escape. This adaptation is frequently seen in lizards, insects, and cephalopods (Burger and Gochfeld 1990, Cooper 2003a, Bateman and Fleming 2011a, Bush 2012, Sugiura 2020).

Figure 2. Examples of morphological adaptations to avoid predation. The animals shown are (left to right): the diabolical ironclad beetle (*Nosoderma diabolicum*), the crested porcupine (*Hystrix cristata*), and the bighorn sheep (*Ovis canadensis*).

3.2 Physiological adaptations: chemical warfare

Unlimited to just morphological adaptations, prey have evolved the use of physiological defense systems to make them unappealing targets of predation. Animals may secrete, contain, or otherwise utilize toxic chemicals that make them unappealing to ingest or even dangerous to the predator's health. Marine animals commonly utilize poison as an antipredator defense, including crustaceans, worms, and fish (Bakus et al. 1986). Poison dart frogs (Dendrobatidae) are an example of a toxic animal which also displays what is called aposematism (Cooper et al. 2009a), or the use of bright coloration to signal to predators that the potential prey is toxic (Caro and Ruxton 2019). Aposematism is common in insects (Sugiura 2020), gastropods (Guilford et al. 2015), and amphibians (Cooper et al. 2009a), but can also be seen in the characteristic black and white coloration of mammals such as skunks (Howell et al. 2021). While bright coloring can send the message of potential toxins, aposematically colored animals are not always toxic as some have evolved aposematism as mimicry to lessen predation risk (Wang et al. 2018). Animals may also wield stings as a manner to transmit toxins to both potential prey and predators alike (for example scorpions, Carlson and Rowe 2009; Hymenoptera, Danneels et al. 2017).

Figure 3. Examples of toxic and aposematically colored animals. Aposematism has evolved as a way for prey to signal to predators an unappetizing or dangerous potential meal. Species shown from left to right are: a poison dart frog (Dendrobatidae), a monarch butterfly caterpillar (*Danaus plexippus*), and a striped skunk (*Mephitis mephitis*).

3.3 Staying hidden: refugia and crypsis

While animals have evolved many morphological and physiological adaptations to avoid predation, some animals avoid predation by simply remaining well-hidden and out of sight. This can be done by utilizing hiding places found in nature, called refugia. These places may provide cover from the sky, blocking aerial predators (Fernández-Juricic et al. 2002), or up trees, preventing capture by terrestrial predators (Cooper 1997, Fernández-Juricic et al. 2002, Møller et al. 2008), or be dense in vegetation, preventing effective chase by predators (Bulova 1994, Cooper 1997, 2003a, Cooper and Whiting 2007, Møller et al. 2008), or be subterranean holes or niches that the predator can't enter (Burger and Gochfeld 1990, MacWhirter 1992, Cooper 2003b, 2009a, Cooper and Whiting 2007). Other species utilize crypsis and imitate their surroundings by using specialized coloration and body shape (camouflage) to blend into the background (Bauwens and Thoen 1981, Cooper 1997, Seltmann et al. 2012, Wilson-Aggarwal et al. 2016, Møller et al. 2019). These animals rely on staying still for as long as possible and remaining undetected by potential predators.

3.4 Behavioral adaptations: to stay and fight or flee

In addition to the species-specific and anatomical and physiological antipredator defenses discussed above, convergent evolution has shaped a generalized behavioral response across taxa to the threat of predation, referred to as general threat responses (Frid and Dill 2002). These behaviors are front-line responses to environmental challenges that can quickly help prey to detect and escape predators. This generalized response presents as a suite of behaviors. The first line of defense is a behavior called vigilance. Vigilance behavior is an attitude of alertness, scanning the environment for possible threats, and is characterized by a raised head and tilted ears (Quenette 1990, Beauchamp 2015). Once an approaching threat is detected, the prey enters alert behavior, and the distance at which the predator is detected is called Alert Distance (AD) (Blumstein et al. 2005, Cooper 2008a, Dumont et al. 2012). Once alert, the prey will continue to monitor the predator, and at some point, if the predation risk is evaluated too high, the prey may decide to flee. The distance at which a predator can approach the prey before it initiates flight is referred to as Flight Initiation Distance (FID) (Frid and Dill 2002, Runyan and Blumstein 2004, Stankowich and Blumstein 2005). Finally, once flight is initiated, the prey will flee for some maximal distance, referred to as Distance Fled (DF) (Cooper 2003a, Bateman and Fleming 2011a, Tätte et al. 2018). For an overview of terminology used to describe the suite of behaviors that occurs during the approach of a predator, see Cooper and Blumstein (2015a).

3.4.a Vigilance behavior

As stated before, vigilance is an active behavior when a prey is scanning the environment for potential threats and occurs prior to the detection of a predator. It is often assumed that vigilance cannot be multitasked with other behaviors (Bednekoff and Ritter 1994, Boland 2003, Childress and Lung 2003), and is therefore exclusive from feeding, resting, and comfort behaviors (ex. grooming). This necessarily means that the amount of time and energy devoted to vigilance comes at a cost to other behaviors and essential functions (Childress and Lung 2003, Dias 2006, Boujja-Miljour et al. 2018). Therefore, the amount of vigilance displayed by an individual is an optimization decision between the potential risks that may be coming and other biological functions that need addressing. Increased vigilance behavior is often assumed to benefit predator detection and avoidance (Burger and Gochfeld 1994, Boland 2003, Childress and Lung 2003, Uchida et al. 2019) although this has rarely been tested (Boland 2003, Fernández et al. 2003), and one study found that vigilance and AD are not correlated (Tätte et al. 2019). Vigilance can be measured in multiple ways: the percentage of time spent vigilant (Bednekoff and Ritter 1994, Boland 2003, Childress and Lung 2003, Carter et al. 2009), the frequency of vigilance bouts or high vigilance postures (Childress and Lung 2003, Carter et al. 2009, Boujja-Miljour et al. 2018), and the duration of vigilance bouts (Burger and Gochfeld 1994, Childress and Lung 2003, Carter et al. 2009).

Many different factors have been shown to alter vigilance levels (for reviews, see Elgar 1989; Frid and Dill 2002). Vigilance often increases when predation risk is higher (Jennings and Evans 1980, Holmes 1984, Beauchamp 2001, Li et al. 2009), for instance when predators are known to be more active (during certain parts of the day, or during certain seasons) (Bednekoff and Ritter 1994, Burger and Gochfeld 1994, Matson et al. 2005, Li et al. 2012, Edwards et al. 2013, Roche and Brown 2013, Boujja-Miljour et al. 2018). Vigilance behavior is also affected by distance from safety (Holmes 1984, DÍaz and Asensio 1991, Bednekoff and Ritter 1994). For instance, female eastern grey kangaroos (*Macropus giganteus*) spend more time in high intensity vigilance when further from cover (Edwards et al. 2013), as do impala (*Aepyceros melampus*) (Matson et al. 2005). Vigilance also varies with age (Holmes 1984, Bednekoff and Ritter 1994, Burger and Gochfeld 1994, Childress and Lung 2003), and body condition (Edwards et al. 2013). Vigilance can vary broadly and with sex and reproductive status. In some species, males are more vigilant than non-reproductive females as these males tend to be more noticeable to predators due to ornamentation and conspicuous territorial behaviors (Fernández et al. 2003, Li et al. 2009), but this is not always the case, as males may take more risks and be vigilant less often when searching for mates or defending territory (Bednekoff and Ritter 1994, Childress and Lung 2003, Li et al. 2012, Boujja-Miljour et al. 2018). Usually, reproductive females have the highest vigilance of all, most likely in preemptive defense of their young (Burger and Gochfeld 1994, Childress and Lung 2003, Carter et al. 2009, Li et al. 2009). Vigilance can also vary with weather, and is particularly influenced by wind which may mask auditory cues of an approaching predator (Cherry and Barton 2017). Forage quality and density can affect vigilance, as animals focusing on consuming high quality forage do not invest as much time into vigilance behavior (Caraco et al. 1980, Boujja-Miljour et al. 2018). Vigilance also varies dominance hierarchy; less dominant individuals are usually in positions that are of lower quality and of higher predation risk, and therefore invest more into vigilance behavior (Li et al. 2012). Urban birds have been found to be more vigilant than rural birds despite lower predation risk, possibly because they must process more sensory information in an urban environment, so the resulting vigilance needs to be directed towards more than an awareness of approaching predators (Tätte et al. 2019). Vigilance can also be reduced during periods of social interactions, such as during aggressive bouts, because these bouts act as a temporary distraction from vigilance behavior (Jakobsson et al. 1995, Brick 1998, Dunn et al. 2004)

3.4.b Alerting and Alert Distance (AD)

The distance at which a prey becomes alert to a potential predator (AD) is a rather less studied antipredator behavior than vigilance or the initiation of flight (FID), perhaps partially due to the fact that alert behavior is not readily observable in many species (Blumstein 2010). Becoming alert to a predator is typically marked by a turn of the head, a focused gaze, or pricking the ears towards the threat (Stankowich and Coss 2006, Cooper 2008a, Tätte et al. 2019). In many cases, the starting distance of the approach from a potential predator is used as a proxy in species where AD is cryptic. And indeed, we must not forget that some species initiate flight as soon as a predator is detected (Powell 1974, Li et al. 2012).

High vigilance levels are commonly assumed to lead to higher AD, yet this association has not been thoroughly proved (Fernández-Juricic and Schroeder 2003, Uchida et al. 2019). Fernández-Juricic and Schroeder (2003) showed that individuals who increased allocation to scanning behavior detected pedestrians earlier, but in another study, more vigilant individuals did not detect predators earlier than less vigilant ones (Tätte et al. 2019). Although relatively under-investigated compared to vigilance, AD has been shown to increase with group size in some species, as more individuals are present to alert to an approaching threat (Hoogland 1981, Brown and Brown 1987, Boland 2003), but not always (Fernández-Juricic and Schroeder 2003). AD is not dependent on the type of threat that approaches (a model predator, a human, a motorized vehicle, etc.), but AD is lower in urban areas possibly because predation risk is lower for many species (except perhaps those targeted by rats and domesticated cats) and less energy is devoted to searching for approaching threats (Uchida et al. 2019). AD decreases when the prey is in an area of high forage quality (Fleming and Bateman 2017), suggesting the prey is less aware of approaching threats when they are focused on foraging. AD increases when approached quickly (Fleming and Bateman 2017), possibly because a faster approach draws more attention. Distractions (such as noise, wind, or conspecifics) have not been found to have an effect on AD, however this was only investigated in one study to date (Yee et al. 2013).

3.4.c Initiating flight and Flight Initiation Distance (FID)

FID, or the distance at which a prey allows a predator to approach before initiating flight, has also been referred to as “flush distance” (in wildlife management), “initial flight distance”, “flight distance”, “escape distance”, and “escape flight distance”. FID is usually considered a standardized estimate of the risk that an individual is willing to take when facing a predator (Lima and Dill 1990, Geist et al. 2005, Stankowich and Blumstein 2005, Blumstein 2006). If the risk is high, prey are expected to initiate flight sooner than if risk is low. The “risk-disturbance hypothesis” (coined by Frid and Dill 2002) predicts that animals should adjust their FID according to the perceived risk of the approaching threat. FID strongly correlates with susceptibility of predation; those with higher susceptibility of predation initiating flight sooner (reviewed in Lima and Dill 1990; Frid and Dill 2002).

Several theories have been proposed to explain the prey risk decision making process in more detail. The first hypothesis is called the “perceptual limit” hypothesis, or the “Flush Early and Avoid the Rush” (FEAR) hypothesis (Blumstein 2010). It predicts that prey should flee as soon as a predator is detected and that logically, flight from a predator is limited only by the ability of a prey to detect an approaching predator (Ydenberg and Dill 1986, Broom and Ruxton 2005). Fleeing immediately from a threat will minimize the risk to the prey as much as is possible (Ydenberg and Dill 1986, Broom and Ruxton 2005), and reduce the costs of predator monitoring (Blumstein 2010). Indeed some animals do flee shortly after threat is detected (female Przewalski's gazelle, *Procapra przewalskii,* Li et al. 2012; starlings, *Sturnus vulgaris*, Powell 1974). A more recent prediction of this hypothesis is that Starting Distance (SD), often assumed to be AD (see section above), will be positively correlated to FID, a prediction which was supported in many bird and mammal species, but not lizards (Samia et al. 2013)

However, if flight is initiated immediately after every threat is detected, this would incur considerable costs as it would significantly impair the prey by interrupting the acquisition of food, territories and/or mates. In situations in which predators are almost omnipresent, always fleeing would result in death or failing to reproduce (imagine accessing a watering hole in Africa, or a colony of breeding birds and their cohort of predators). In contrast, "Escape Theory" proposes that FID has evolved as an economic calculation where the perceived predation risk is assessed, and flight initiated only when the costs of fleeing and the costs of remaining become equal (Ydenberg and Dill 1986). Escape theory also accounts for increasing site fidelity and the associated costs of fleeing (Ydenberg and Dill 1986). If the territory a prey occupies is of high value, it may delay flight as long as possible in order to avoid losses of opportunity (Lima and Dill 1990, Stankowich and Blumstein 2005). This would be the case for brooding birds, basking ectotherms, or animals defending sites of high foraging or mate quality (Rand 1964, Cooper 1997, 2003a, 2009b, Cooper et al. 2003, Beale and Monaghan 2004a, Cooper and Wilson 2007, Li et al. 2012, Samia et al. 2016, Arroyo et al. 2017, Fleming and Bateman 2017, Dowling and Bonier 2018, Ventura et al. 2021). For example, foraging waterstriders (*Gerris remiges*) had shorter FID when their captured prey was larger(Ydenberg and Dill 1986). FIDs were also shorter for Bonaire whiptail lizards (*Cnemidophorus murinus*) in the presence of food (Cooper et al. 2003), and for male broad-headed skinks (*Eumeces laticeps*) in the presence of a female (Cooper 1997). Immediate flight is only predicted when the predator is closer than the optimal FID (Ydenberg and Dill 1986, Blumstein 2003, Cooper 2005, 2008b), and prey should maintain this distance from predator through flight – called the "margin of safety hypothesis" (seen in Columbian back-tailed deer, *Odocoileus hemionus,* Stankowich and Coss 2006). Flight should only occur when the benefits of staying equal the costs of leaving, and flight should be initiated immediately if the predator crosses the threshold (Stankowich and Coss 2006). Finally, "optimal escape decisions" develops this idea further by changing escape theory from a break-even model to an optimality model that concludes there may be fitness benefits above the cost=benefits calculation (Cooper and Frederick 2007). Due to these theories, there are three separate zones of reaction predicted between the prey and predator: Zone I, where the predator is within a minimum distance where all targeted prey will initiate flight; Zone II, where the predator is in a range of distance where targeted prey will monitor and optimize the costs of fleeing vs. those of staying; and Zone III where the predator is at such a distance that no disturbance is caused, either because there is no perceived risk, or the predator was not detected (Blumstein 2003, Bateman and Fleming 2011b).

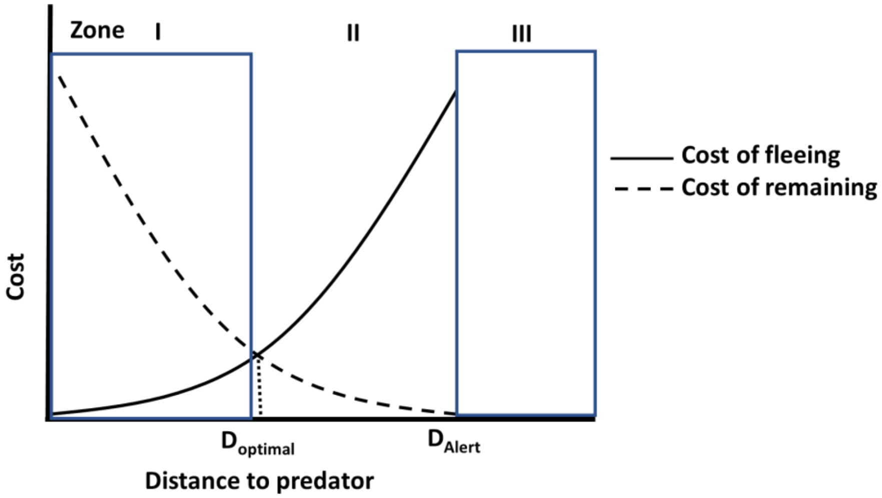


Figure 4. The economic calculation of the costs of fleeing vs. the costs of staying based on escape theory. The cost of remaining (or the benefit of fleeing, dashed line) increases as the predator nears, while the cost of fleeing (solid line), which necessitates the interruption of ongoing behaviors, decreases as the predator nears. The intersection between the two functions defines the cost-minimized location of the optimal flight initiation distance. There are three zones of prey reaction. In Zone I, which is below the optimal flight initiation distance, the prey will always initiate flight as soon as a predator is detected. In Zone II, the prey is aware of the presence of the predator and will monitor the predator to optimize the costs of fleeing vs. those of staying. In Zone III, no disturbance is caused because there is either no perceived risk or the predator has not been detected yet. Modified from Blumstein (2003).

3.4.c.i Flight initiation distance and perceived risk

As discussed previously, FID is thought of a measure of the perceived risk to the focal individual (reviewed in Frid and Dill 2002; Stankowich and Blumstein 2005). If the focal individual evaluates higher risk, they will have longer FID, if they evaluate less risk, they will have a shorter FID. Many things can alter perceived risk such as the predator type (Burger 1998, Berger et al. 2007, Uchida et al. 2019), size (Samia et al. 2016), and number of predators (Burger and Gochfeld 1991). Crimson rosellas (*Platycerus elegans*) were found to flee sooner when approached by two people instead of one (Geist et al. 2005). Similar results were found by (Beale and Monaghan 2004b) in kittiwakes, *Rissa tridactyla.* There are also actions that can communicate the intent of a predator, such as the focus of the predator's gaze (Burger and Gochfeld 1981, 1990, Cooper 2003b, Bateman and Fleming 2011b, Sreekar and Quader 2013, Samia et al. 2016). Speed of approach produces consistently strong results with faster speeds of approach increasing FID in many cases, suggesting it is a cue that poses a significant threat to the prey animal (Cooper 1997, 2003b, 2006, Burger 1998, Cooper et al. 2003, 2009a, 2009b, Stankowich and Blumstein 2005, Stankowich and Coss 2006, Cooper and Whiting 2007, Bateman and Fleming 2011b, Samia et al. 2016). Finally, directness of approach is another similarly common finding, with more direct approaches increasing FID (Burger and Gochfeld 1981, Bulova 1994, Cooper 1997, 2003b, Cooper et al. 2003, 2009a, Stankowich and Blumstein 2005, Stankowich and Coss 2006, Cooper and Whiting 2007, Smith-Castro and Rodewald 2010, Sreekar and Quader 2013, Samia et al. 2016).

3.4.c.ii Flight initiation distance as a species-specific trait

FID is a species-specific value (Burger and Gochfeld 1991, Bulova 1994, Rodgers and Smith 1995, 1997, Blumstein et al. 2003, Blumstein 2006, Møller 2008, Díaz et al. 2013, 2021, Samia et al. 2015), interspecific variation in FID is altered by body size (larger animals can perceive threats at longer distances, may be under greater predation risk due to greater visibility, and also possess greater capabilities of flight over larger distances, yet also suffer higher costs of flight) (Burger and Gochfeld 1991, Bulova 1994, Fernández-Juricic et al. 2002, Rodgers and Schwikert 2002, Blumstein et al. 2005, Stankowich and Blumstein 2005, Blumstein 2006, Møller 2008, Díaz et al. 2013, 2021, Samia et al. 2015, Piratelli et al. 2015, Tablado et al. 2021), taxonomic level (Rodgers and Schwikert 2002, Blumstein et al. 2005, Blumstein 2006, Díaz et al. 2013, Samia et al. 2015), latitude (mean FID decreases with increasing latitude) (Díaz et al. 2013, 2021, Tablado et al. 2021), diet (mixed results – some studies find flightiness is more common for herbivores, while others suggest it is more likely to evolve in omnivorous/carnivorous species) (Blumstein 2006, Makin et al. 2017, Díaz et al. 2021), reproductive system and age of first reproduction (longer lived species take smaller risks, invest more in self-maintenance and less in reproduction) (Rodgers and Schwikert 2002, Blumstein 2006, Samia et al. 2015), human disturbance (FIDs are frequently shorter in urban environments – discussed below) (Burger and Gochfeld 1991, Blumstein et al. 2005, Møller 2008, Díaz et al. 2013, 2021, Piratelli et al. 2015, Samia et al. 2015, Tablado et al. 2021), history of hunting (hunted animals usually display longer FID – discussed below), and migratory status (migratory birds tend to have longer FID) (Burger and Gochfeld 1991). Prey having evolved antipredator defenses including physical defenses, camouflage, and the use of refugia often have shorter FIDs as they rely on alternate strategies to prevent predation (Fernández-Juricic et al. 2002, Stankowich and Blumstein 2005, Samia et al. 2015, Wilson-Aggarwal et al. 2016) which are unlikely to have evolved independently from flight behavior. For instance, aposematically colored poison dart frogs (*Dendrobates auratus* and *Oophaga pumilio*) show reduced escape behavior (Cooper et al. 2009a). Bird species with cryptically colored plumage have consistently shorter FID than brightly colored closely related species (Møller et al. 2019), and armored brook sticklebacks, *Culea inconstans*, are less responsive to the presence of a predator than fathead minnows, *Pimephales promelas* (Abrahams 1995).

3.4.c.iii Flight initiation distance and individual characteristics

There are also numerous individual-specific causes for variation in FID (reviewed in Frid and Dill 2002). One such factor is age, with juveniles frequently showing shorter FIDs that increase with experience (Berger et al. 2007, Seltmann et al. 2012, Kalb et al. 2019, Møller et al. 2019). As such, previous exposure to a predator can have impacts on FID, either through sensitization or habituation (Burger and Gochfeld 1990, Stankowich and Blumstein 2005, Samia et al. 2016). Individuals in areas of high forage quality show reductions in FID (Fleming and Bateman 2017). Animals in better body condition take fewer risks and display longer FID (Beale and Monaghan 2004a, Seltmann et al. 2012). For example, yellow-bellied marmots, *Marmota flaviventris*, in better body condition had longer FID, consistent with the idea that animals in better body condition are more conservative risk-takers, while those with poor body condition may take more risks in order to allow more time to forage (Petelle et al. 2013). Larger individuals frequently have longer FID (Burger and Gochfeld 1990, Sreekar and Quader 2013, Møller 2014, Tablado et al. 2021). Levels of stress hormone, such as corticosterone, may also affect FID, although the direction of the effect may vary between and within studies (Seltmann et al. 2012; but see Tablado et al. 2021). Dominance may influence FID as well, with more dominant individuals usually occupying better territories with lower predation risk and therefore have shorter FID (Ekman 1987). The size of social groups also generally impacts FID, and this will be discussed further below (Fernández-Juricic et al. 2002). Weather and temperature may affect FID (Bulova 1994, Fernández-Juricic et al. 2002, Cooper 2003b, Díaz et al. 2021). Temperature is crucial to the FID of ectotherms (Rand 1964, Bulova 1994, Samia et al. 2016), and also to other animals that are sensitive to temperature, such as incubating birds. In ground nesting birds (five Charadriidae and three Camprimulgidae), flight initiation distance was shorter during mid-day, showing reduced tendency to abandon the eggs when the temperature was unfavorable for prolonged exposure, suggesting escape behavior was mediated by thermal regulation (Wilson-Aggarwal et al. 2016). Time of day may also impact FID, since predators may be more or less active at different times of day therefore altering predation risk (Burger and Gochfeld 1991, Bulova 1994, de Jong et al. 2013, Petelle et al. 2013, Piratelli et al. 2015, Wilson-Aggarwal et al. 2016, Ferguson et al. 2019). Season may similarly have an impact on FID due to changes in predator distribution, abundance, or activity (de Jong et al. 2013). Finally, prey show shorter FID when close to refugia or cover (Burger and Gochfeld 1990, Bulova 1994, Cooper 1997, 2003b, Fernández-Juricic et al. 2002, Stankowich and Blumstein 2005, Cooper and Whiting 2007, Møller et al. 2008, Cooper et al. 2009a, Tablado et al. 2021). Sex and reproduction often have an effect on FID, and in various different directions. In species with males who have increased conspicuousness due to their ornamentation, males often show increased FID (Petelle et al. 2013). For example in common pheasants, *Phasianus colchicus*, and golden pheasants, *Chrysolophus pictus*, males have longer FID than the more cryptically colored juveniles and adult females (Møller et al. 2019). Yet, males will reduce FID in the presence of a female (Sreekar and Quader 2013, Ventura et al. 2021), or may be aposematically colored to reduce predation (Kalb et al. 2019). Females with young and reproductive adults tend to reduce flight behavior in order to stay and defend nests or offspring (Bauwens and Thoen 1981, Samia et al. 2016, Arroyo et al. 2017).

3.4.c.iv Flight initiation distance and reproduction

Reproductive animals incur an increased fitness cost of fleeing, since fleeing could result in the loss of current reproduction. It is common to see reduced FIDs in reproductive animals. As an example, many water birds display shorter FIDs while nesting than while foraging (Rodgers and Smith 1997), and bald eagles (*Haliaeetus leucocephalus*) have shorter FID when nesting compared to those foraging or perching (Grubb and King 1991). Nesting snowy plovers (*Charadrius alexandrinus*) have half the FID of non-reproductive wintering plovers (Lafferty 2001). Parental commitment to offspring is expected to increase, and FID decrease, as the probability of successful reproduction increases (de Jong et al. 2013, Arroyo et al. 2017, Dowling and Bonier 2018). Parents are thought to be less susceptible to initiate flight and have shorter FIDs if residual reproductive value is high, with larger clutch sizes, if offspring are likely to survive until independence, and if the brood is of high value (Trivers 1972, Montgomerie and Weatherhead 1988, Clark and Ydenberg 1990a, 1990b, Frid and Dill 2002, Lima 2009, Dowling and Bonier 2018). As offspring age, their likelihood of survival to independence increases, as do their energy requirements and parental effort in procuring resources (thus, brood value increases), and so parents are thought to increasingly reduce flight behaviors and increase brood defense (Barash 1975, Andersson et al. 1980, Ackerman and Eadie 2003, Redmond et al. 2009, Svagelj et al. 2012). It is relatively common for incubating and brooding penguins to have FIDs of 0 as they stay and defend the brood aggressively rather than flee, something that is not seen during other life history stages (Humboldt penguins, *Spheniscus* *humboldti*, (Ellenberg et al. 2006), yellow-eyed penguins, *Megadyptes antipodes*, (Ellenberg et al. 2009, 2013), Magellanic penguins, *Spheniscus magellanicus,* (Yorio and Boersma 1992, Fowler 1999, Villanueva et al. 2014), Gentoo, *Pygoscelis papua*, Royal, *Eudyptes schlegeli*, and king penguins, *Aptenodytes patagonicus* (Holmes 2007), African penguins (*Spheniscus dermersus*) (Pichegru et al. 2016).

Although parental FIDs tend to reduce as offspring age and brood value increases, maximal FID reduction is dependent on the intersection of offspring vulnerability and highest brood value (Barash 1975, Andersson et al. 1980). Vulnerability of the offspring relies on whether the offspring is born/hatched precocial or altricial. Precocial offspring are rapidly able to mount independent antipredator behaviors, while altricial offspring remain necessarily dependent on their parents for protection from predators. In species with precocial young, FID is usually the shortest immediately after hatching and increases quickly as offspring gain autonomy (killdeer, *Charadrius vociferus,* Brunton 1990; willow ptarmigan, *Lagopus lagopus,* Sandercock 1994; Savanna nightjar, *Caprimulgus affinis,* Tseng et al. 2017). In these species, the precocial young are mobile and able to scatter upon the approach of a predator (Andersson et al. 1980, Buitron 1983, Sandercock 1994). Since usually only one offspring can be taken by a predator at a time, and offspring can independently flee, parental defense is no longer as efficient at this time and greatly reduces. For altricial offspring, investment in brood defense and a reduction of FID continues as the brood ages, since the brood is still reliant on parental care and defense. Maximal parental investment, and the shortest FIDs, occur just before fledging/weaning when offspring gain a measure of independence and self-mobility (seen in fieldfare, *Turdus pilaris,* Andersson et al. 1980; Adélie Penguins, *Pugoscelis adeliae,* Wilson et al. 1991; meadow pipit, *Anthus pratensis,* Pavel 2006; African penguin, *Spheniscus demersus,* Pichegru et al. 2016). In species such as penguins, whose altricial young rely on parental care for thermal regulation, interruptions of care could greatly increase the risk of nest failure.

Timing of reproduction may also have impacts on the FID of parents, as rates of successful breeding may vary greatly between early and late breeding attempts. In some species, there is high re-nesting potential and therefore parents should commit less effort into nest defense and have longer FID than species with low re-nesting potential (Dawkins and Carlisle 1976, Boucher 1977, Weatherhead 1979, Svagelj et al. 2012). In other species, the likelihood of successful fledging/weaning drastically declines as the breeding season advances. If late breeding attempts result in offspring that have a lower probability of survival, then late broods should have lower brood value and parents will have lesser FID reductions than when caring for early broods (Barash 1975, Andersson et al. 1980, Kleindorfer et al. 1996, Tryjanowski and Goławski 2004). For example, when presented with a stuffed black-billed magpie, *Pica*

pica, house sparrows, *Passer domesticus*, were more likely to stay and defend earlier (and the more successful) broods (Klvaňová et al. 2011).

3.4.d Distance Fled, DF

After a predator is detected and flight is initiated, the prey will flee for a certain distance (Distance Fled, DF), before reassessing the situation. DF is also sometimes referred to as Final Flight Distance. This behavior is also understudied, but more information is available than AD, for example. Typically, DF is related to distance to refuge as refuges are the usual objective of flight, but is also dependent on the presence of obstacles along the path, and capacity of the terrain for greater run speeds (Samia et al. 2016, Tätte et al. 2018). Cooper and Peréz-Mellado (2004) suggest that DF might be similarly affected by the relationship between perceived risk and cost of escape, with less costly flights and riskier perceived threats resulting in longer DFs. In their study, Balearic lizards, *Podarcis lilfordi*, fled shorter distances when food was present (Cooper and Peréz-Mellado 2004). DFs tend to be longer when the perceived risk is higher and FIDs longer (Tätte et al. 2018), for example many wildlife species were found to flee farther when a pedestrian is accompanied by a dog, a situation which is perceived as more risky than a pedestrian alone (Knight and Miller 1996). Additionally, birds in rural habitats escaped further (Tätte et al. 2018), suggesting that habituation and the accompanying reduction in predation risk affects DF as well as FID. Lizards with autotomized tails fled further than lizards with intact tails, possibly because they could not rely on alternative methods of predation reduction and their predation risk was increased (Cooper 2003a). Gravid female lizards also run less far, but this is likely due to physical restrictions (Bulova 1994).

3.4.e Defense and aggression

A last behavioral defense against predation is staying to fight. The use of aggression limits the ability of the prey to flee, as they are mutually exclusive behaviors. The use of aggression is also more dangerous than fleeing, as it necessitates confronting the predator and can result in injury. Aggression is seen in animals that possess armaments for fighting against predators (examples: scorpions, Carlson and Rowe 2009; crabs and lobsters Barshaw et al. 2003; horned/antlered mammals, Packer 1983; Stankowich and Caro 2009). Yet, aggression is also commonly seen in reproductive animals who chose to stay and defend their offspring over fleeing and sacrificing current reproduction. In African penguins, *Spheniscus dermersus*, parents with chicks were more aggressive towards the approaching human than incubating birds, suggesting parental antipredator decisions were linked to brood age (Pichegru et al. 2016). Finally, mobbing, or the surrounding of a predator by prey who then proceed to aggressively harass the predator, is a tactic that is sometimes used in group-living species. Meerkats, *Suricata suricatta*, are one of these species that commonly uses mobbing in order to prevent predation (Graw and Manser 2007). Mobbing is also seen in bank swallows, *Riparia riparia*, (Hoogland and Sherman 1976), cliff swallows, *Hirundo pyrrhonata*, (Brown and Brown 1987), and white-tailed and black-tailed prairie dogs, *Cynomys leucurus and Cynomys ludocivianus,* (Hoogland 1981), for example.

4. The evolution of group living as a response to predation: effects on antipredator behavior

Although social groupings may form for a variety of reasons, one of the main hypothesis proposed for the formation of social groups is defense against predation (Alexander 1974, Brown and Brown 1987, Cresswell 1994). Grouping can benefit in many ways. First, having more individuals in a group means more individuals are available to scan for predators at any given time (the "many-eyes hypothesis", Pulliam 1973; Lima and Dill 1990). Also, as many predators can only claim one individual at a time, the chance that each individual prey will be the target of predation reduces with increasing group size (the "dilution effect hypothesis", Dehn 1990; Roberts 1996; Bednekoff and Lima 1998). There are numerous examples of groups forming in order to immediately reduce predation risk and benefit from increased number of individuals. For example, when foraging levels are sufficiently high, solitary house sparrows (*Passer domesticus*) will call others to join them, hence forming a flock and increasing safety while foraging (Elgar 1986). Group size has been found to increase when alarm calls are given (Ekman 1987), increase in the presence of a predator (Caraco et al. 1980, Carere et al. 2009, Makin et al. 2017), and decrease when individuals are foraging in order to limit food competition (Elgar 1986, Van Havre and Fitzgerald 1988). In another example, emus (*Dromaius novaehollandiae)* will cluster when an approaching threat has been detected, and then run away in a tight flock (Boland 2003), as will starlings, *Sturnus vulgaris* (Carere et al. 2009). Yet, while grouping may dilute predation risk and promote early detection of predators, large groups are also more conspicuous to predators and may draw extra attention, and they also face increased competition (for space, mates, and food), and increase the transmission of infectious diseases such as parasites (Hoogland and Sherman 1976, Hoogland 1981, Clode 1993, Hebblewhite and Pletscher 2002, Altizer et al. 2003). Below, I shall discuss the various hypotheses on how grouping alters the various antipredator behaviors (vigilance, AD, and FID) that we have discussed so far.

4.1 Vigilance and group size, the group-size effect

It is a widely replicated observation that individuals spend less time being vigilant with increasing group size, despite an increasing level of corporate vigilance, called the "group size effect" (Pulliam 1973, Elgar 1989, Quenette 1990, Lima 1995). The group size effect has been demonstrated in mammals (Holmes 1984, Bednekoff and Ritter 1994, Burger and Gochfeld 1994, Childress and Lung 2003, Fairbanks and Dobson 2007, Rieucau and Martin 2008, Taraborelli 2008, Carter et al. 2009, Li et al. 2009, 2012), birds (Powell 1974, Lazarus 1978, Caraco et al. 1980, Elgar et al. 1984, DÍaz and Asensio 1991, Lima 1995, Boland 2003, Fernández et al. 2003, Randler 2005, Dias 2006, Boujja-Miljour et al. 2018), and through mathematical models (Beauchamp 2001, 2015, 2017) (reviewed in Lima and Dill 1990).

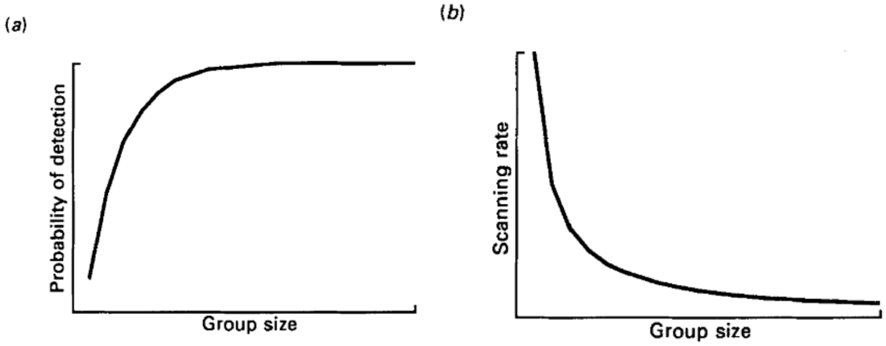


Figure 5. The relationship between group size, predator detection and scanning rate (vigilance behavior). a) The probability of predator detection increases with group size, while in b) vigilance decreases with group size. Reproduced from (Elgar 1989).

4.2 On the advantages of group living in regards to predation

4.2.a The "selfish herd" hypothesis

The selfish herd hypothesis provides insight both into how social groupings might form, and how individuals can benefit from predator avoidance when joining a group (Hamilton 1971). This hypothesis suggests that a third individual will join a group of two individuals by placing themselves in the gap between the first two (Hamilton 1971). Being surrounded by neighbors provides a shield against predatory attacks, as the neighbors are more likely targets of predation. An individual who is alone for quite a distance will find itself the sole target of predation, and thus when provided the chance, will try to maneuver itself into the gap between two other individuals. Looking at Atlantic silversides, *Menidia menidia*, stragglers were more frequently attacked by predators and suffered significantly higher predation risk (Parrish 1989), as were more spaced redshanks, *Tringa totanus*, within the flock (Quinn and Cresswell 2006). Maneuvering into the gaps between individuals will not only cause a group to form, but also clarifies movements of individuals with groups as individuals attempt to centralize their position. Many species show a closing in, or aggregation, of their group upon the approach of a predator (Viscido et al. 2001, Viscido and Wethey 2002, Boland 2003, Quinn and Cresswell 2006, Carere et al. 2009, King et al. 2012). This was demonstrated nicely in an experiment by Krause (1993), where a single minnow (*Phoxinus phoxinus*) was shown to consistently position itself within the center of a shoal of dace (*Leuciscus leuciscus*) when a threat was introduced.

The assumption of the selfish herd hypothesis is that individuals on the outside of a group are the most susceptible to predation, as they are the first individuals encountered by an approaching predator, and as such should be the most vigilant (Jennings and Evans 1980, Burger and Gochfeld 1994, Morton et al. 1994, Reluga and Viscido 2005, Dias 2006, Fairbanks and Dobson 2007, Morrell et al. 2011). Indeed, it is true that individuals on the edge of a social group tend to be more vigilant than those in the center, termed the “edge effect” (Pulliam 1973, Inglis and Lazarus 1981). Impala (*Aepyceros melampus*) on the periphery of the group were more vigilant than those in the center (Matson et al. 2005), as were springbok, *Antidorcas marsupialis* (Bednekoff and Ritter 1994), starlings, *Sturnus vulgaris* (Jennings and Evans 1980), and coots, *Fulica atra* (Randler 2005). In willow tits, *Parus montanus*, the more vigilant edge birds were also subordinate members of the flock which implies territory is allocated by a dominance hierarchy (Ekman 1987). The selfish herd effect is also suggested as an explanation for uneven breeding success between center and edge nests of groups, for example in colonially breeding bank swallows, *Riparia riparia* (Hoogland and Sherman 1976), and yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Picman et al. 2002). In colonial orb-weaver spiders (*Meteperira incrassata*), larger spiders and females guarding egg sacs are more commonly found in the center of the colony and have higher reproductive success, despite the fact that prey availability is higher on the periphery, likely because predation risk is also significantly higher on the periphery (Rayor and Uetz 1990).

Strong edge effects are also seen in colonies of penguins, for example in Adélie penguin (*Pygoscelis adeliae*), nests located on the edge of the colony face much lower reproductive success due to increased predation risk (Giese 1996, McDowall and Lynch 2019). Another study found that reproductive success was lower and nest predation was higher in smaller colonies than larger colonies of Adélie penguin (*Pygoscelis adeliae*) due to an increase of perimeter-to-area- ratio, thereby increasing the relative number of peripheral nests (Schmidt et al. 2021). Similarly, predation attempts on penguin chicks were 4.1-7.9x more frequent on the colony edge than in the center in Adélie penguin (*Pygoscelis adeliae*) and Gentoo penguins (*Pygoscelis papua*) (Emslie et al. 1995). In king penguins (*Aptenodytes patagonicus*), peripheral birds in the colony have greatly reduced reproductive success, possibly because peripheral breeding birds have about twice as many interactions with predators than central birds (Côté 2000, Descamps et al. 2005). Peripheral position in the colony also tend to be claimed by late breeding birds, which may contribute to the low reproductive success rate of late breeding birds in this species (Côté 2000). Yet, a similar study found no difference in breeding success between central and peripherally breeding king penguins (Descamps et al. 2009).

4.2.b The "many-eyes" hypothesis

The many-eyes hypothesis, also called the "detection effect", predicts that animals in groupings are able to detect the approach of a threat much earlier than solitary animals owing to the presence of more individuals who are able to scan the environment for predators at any point in time (Pulliam 1973, Caraco et al. 1980, Lima 1995). One assumption of this hypothesis is that all member of the group are alerted to an attack as long as it is detected by one individual, although evidence for this is scarce and rarely tested (Lima 1995), except in species where alarm calls are used (starlings, *Sturnus vulgaris,* Powell 1974; Columbian ground squirrels, *Spermophilus columbianus,* Fairbanks and Dobson 2007; Belding's ground squirrel, *Spermophilus beldingi,* Sherman 1985; meerkats, *Suricata suricatta*, (Townsend et al. 2012). A second assumption is that individuals in the group must monitor groupmates for information, and there is evidence that individuals monitor the actions of their closest groupmates (Lima 1995). The many eyes hypothesis can also apply to denser groupings as well as larger groupings, as individuals pay attention to their closest neighbors (Elgar et al. 1984, Burger and Gochfeld 1991, Randler 2005). The many-eyes hypothesis has been found in many animal groups (Hoogland 1981, Cresswell 1994, Boland 2003, Fairbanks and Dobson 2007, Taraborelli 2008) and models (Dehn 1990, Beauchamp 2017). While larger groups can detect approaching predators sooner (longer AD) (Kenward 1978; Hoogland 1981; Ydenberg and Dill 1986, but see Fernández-Juricic and Schroeder 2003), it is unclear how this affects FID. Longer FID were observed in groups of starlings (*Sturnus vulgaris*) (Powell 1974), longer AD, FID, and DF were observed in larger groups of caribou, *Rangifer tarandus* (Aastrup 2000), migratory birds in India (Burger and Gochfeld 1991), 17 species of Estonian bird (Tätte et al. 2018), 10 species of waterbird (Mayer et al. 2019), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) (De Boer et al. 2004). Yet, for the black redstart (*Phoenicurus ochruros*), there was no effect of flock size on FID (Kalb et al. 2019), and for emus, *Dromaius novaehollandiae* (Boland 2003), and impala, *Aepyceros melampus* (Matson et al. 2005), FID decreased with group size.

4.2.c The "dilution effect" hypothesis

If a predator can only attack and kill one individual prey at a time, being in a larger group dilutes the individual risk of predation (Inman and Krebs 1987, Dehn 1990). For example, goshawks can only target a single pigeon at a time (Kenward 1978). This scenario, termed the “dilution effect” predicts that FID should be lowered in larger groups due to reduced individual risk of predation. The dilution effect has been supported in many animal species (Cresswell 1994, Lucas and Brodeur 2001, Boland 2003, Fernández et al. 2003, Duca et al. 2019) and is predicted by multiple models (Bednekoff and Lima 1998, Beauchamp 2017). When in larger groups, FID tends to decrease due to the reduced risk of an individual being the target of a predation attempt (Fernández-Juricic et al. 2002, Stankowich and Blumstein 2005, Tablado et al. 2021). The dilution effect is thought to play a role in largescale occurrences, such as in the synchronization of migration and nesting times, or the formation of breeding colonies (Hoogland and Sherman 1976, Wiklund and Andersson 1994, Danchin and Wagner 1997, Hernández-Matías et al. 2003, Harts et al. 2016, Duca et al. 2019). Yet, the formation of such large groupings can have a negative drawback, as they are easier to see and be detected by predators, and may in fact, draw undue attention (Clode 1993, Hebblewhite and Pletscher 2002).

4.3 *On the costs of group living in regards to predation*

4.3.a The “distracted prey” hypothesis

The “distracted prey” hypothesis proposes that any stimulus an animal can perceive is capable of distracting the individual by reallocating part of its finite attention, thus preventing it from responding to an approaching threat (Chan et al. 2010). White noise increases blue-tailed skink (*Emoia impar*) vigilance behavior but had no impact on FID, hence it neither distracted skinks or impaired their risk assessment (Kelligrew et al. 2021). While these disturbances can be man-made, for example the white noise seen in Chan et al. (2010) and Petrelli et al. (2017), distraction may also come in the form of social interactions (Brick 1998, Li et al. 2012). Striped plateau lizards, *Sceloporus virgatus*, had shorter FID when interacting with other members of the same species (Cooper and Wilson 2007, Cooper 2009b), as did brown anoles, *Anolis sagrei* (Yee et al. 2013). Lizards consistently allow closer approach of predators when conspecifics are present (Samia et al. 2016). European robins, *Erithacus rubecula*, that were engaged in combat were slower to react to a simulated predatory attack (Dunn et al. 2004), as were the cichlid fish, *Neolamprologus pulcher* (Hess et al. 2016). Another study showed the same results for the willow warbler, *Phylloscopus trochilus*, and a South American cichlid fish, *Nannacara anomala* (Jakobsson et al. 1995). However, it is not just aggressive social interactions that impair predator detection, in impala (*Aepyceros melampus*) allogrooming was found to reduce the responsiveness of the deliverer (Mooring and Hart 1995)

4.4 Group antipredator hypotheses working in concert

All of these hypotheses are non-mutually exclusive and may act in concert on a population. Many studies have looked at the joint relationship between the dilution effect and many-eyes hypotheses, finding mixed results. Emus, *Dromaius novaehollandiae*, were found to benefit from both the dilution effect and many-eyes hypothesis (Boland 2003), while elk, *Cervus elaphus*, were found to benefit more from the dilution effect (Hebblewhite and Pletscher 2002), and Columbian ground squirrels were found to benefit most from the many-eyes effect (Fairbanks and Dobson 2007). For zebras (*Equus quagga*), the many-eyes hypothesis was of more importance than dilution effects in mixed species herds, but only when the species shared a common predator (Schmitt et al. 2014). In bighorn sheep (*Ovis canadensis*), lactating ewes relied solely on the many-eyes hypothesis, while barren ewes benefited from both many-eyes and the dilution effect (Rieucau and Martin 2008). While studies comparing the many-eyes hypothesis and the dilution effect are common (for a model that takes both into account, called “attack abatement”, see Turner and Pitcher, 1986), no such study has also explored conjointly the selfish herd or distraction hypothesis.

5. Antipredator behaviors with respect to animal personality

Animal personality is defined as any behavioral trait that is repeatable and over time and contexts (Sih et al. 2004b, Réale et al. 2007, Dingemanse and Wright 2020). Repeatability requires that each individual has a unique value for a behavioral trait and that it can be consistently measured. It requires both low-within and high-between individual variation in behavior in order to be repeatable (Highcock and Carter 2014). Mathematically, repeatability is calculated as $r = \sigma^2_\alpha / (\sigma^2_\alpha + \sigma^2_\varepsilon)$ where σ^2_α is the variance among individuals, and σ^2_ε is the variance within individuals (Bell et al. 2009). This means that repeatability will not be observed if i) each individual displays high amounts of variation in the behavioral trait, or ii) each individual has similar values of the behavioral trait. In other words, it is necessary that individuals behave consistently and differently from other animals.

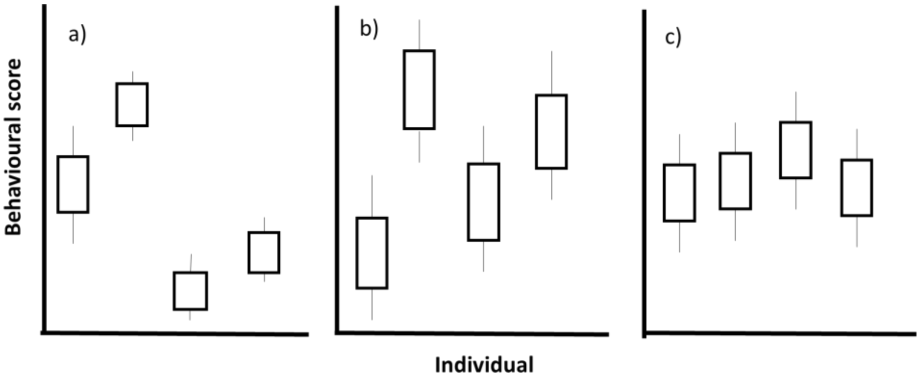


Figure 6. Representations of repeatable measures and non-repeatable measures. a) This figure shows behavioral scores that have low-within and high-between individual variation, meaning this data set is likely repeatable. b) This figure has high-within individual variation, meaning each individual is not distinguishable from the next due to high overlap in behavioral scores. c) This figure shows low-between individual behavioral scores. Each individual is making consistent, but similar behavioral decisions, and so once again a personality cannot be distinguished between individuals.

Personality traits can be genetically determined (Van Oers et al. 2004, van Dongen et al. 2015), and can therefore be inherited (Réale et al. 2000, Dingemanse et al. 2002, Bize et al. 2012, Møller 2014, Lartigue et al. 2021). In fact, the repeatability of a trait sets the upper limit for its heritability (Falconer and Mackay 1996, Réale et al. 2000). According to Réale et al. (2007), there are five major personality gradients: shyness-boldness, exploration-avoidance, activity, sociability, and aggressiveness. Shyness-boldness is an individual's reaction to any risky situation, unless it is a new situation, which would fall under exploration-avoidance (Wilson et al. 1994, Réale et al. 2007). As FID is associated with risk assessment and risk taking when facing a predator or a threatening disturbance (Lima and Dill 1990, Geist et al. 2005, Stankowich and Blumstein 2005, Blumstein 2006), it is frequently used to explore boldness as a personality trait (Carter et al. 2010, 2012, Evans et al. 2010, Atwell et al. 2012, Petelle et al. 2013, Highcock and Carter 2014, Young et al. 2015, Arroyo et al. 2017). And, indeed, FID is frequently repeatable: burrowing owls, *Athene cunicularia*, r = 0.82-0.92 (Carrete and Tella 2010); yearling yellow-bellied marmots, *Marmota flaviventris,* r = 0.40 (Petelle et al. 2013); wild horses, *Equus caballus*, r = 0.42 (Cabrera et al. 2017); Namibian rock agama, *Agama planiceps*, r = 0.71, (Carter et al. 2012); barn swallows, *Hirundo rustica*, r = 0.62 (Møller 2014); female eiders, *Somateria mollissima*, within year between r = 0.76–0.80, and between years r = 0.37-0.69, (Seltmann et al. 2012); black swans, *Cygnus atratus*, r = 0.61 (van Dongen et al. 2015). Bolder individuals tend to do better in areas of high human disturbance (Carrete and Tella

2010, Evans et al. 2010, Atwell et al. 2012, Arroyo et al. 2017) as the resulting disturbances in bold individuals are reduced compared to shy individuals.

The repeatability of AD has not been explored to date, but the repeatability of vigilance has been tested in some studies and found to be slightly repeatable. In female eastern grey kangaroos (*Macropus giganteus*), 7% of the variation in total time vigilant and 14% of the variance in vigilance intensity was explained by individual identity (Edwards et al. 2013). House sparrow (*Passer domesticus*), had an r = 0.13 for duration spent vigilant, r = 0.16 for the frequency of vigilance bouts, and r = 0.22 for the variation in the duration of vigilance bouts (Boujja-Miljour et al. 2018). Common redshanks, *Tringa totanus*, had an r=0.21 for vigilance rates (Couchoux and Cresswell 2012).

While repeatability is required for there to be a personality trait, behavioral traits are still flexible and may be altered as a result of repeated approaches, a process which is necessary to measure repeatability (Highcock and Carter 2014). Typically, when populations of animals are repeatedly exposed to threats that are not very risky and predictable (Knight and Miller 1996, Rodríguez-Prieto et al. 2010), animals tend to habituate to the threat by reducing FIDs (Burger and Gochfeld 1981, 1990, Fernández-Juricic et al. 2002, Carter et al. 2012, Petelle et al. 2013, Cabrera et al. 2017, Fleming and Bateman 2017, Uchida et al. 2019). If a prey animal initiated flight every time a common, non-dangerous predator was seen, this would be a very costly behavior that would hinder their ability to find time and energy to forage or engage in self-care behaviors (Rodríguez-Prieto et al. 2010, Fleming and Bateman 2017). In fact, in Iberian wall lizards, *Podarcis hispanica*, individuals that habituated more readily to a frequent, predictable, low risk predatory stimulus were able to maintain better body condition than individuals that did not habituate as readily (Rodríguez-Prieto et al. 2010). Generally, habituation is observed in places highly disturbed by human activities, for example in urban environments (Stankowich and Blumstein 2005, Evans et al. 2010, Piratelli et al. 2015, Tablado et al. 2021). Møller (2008) tested 44 common species of European birds and found that urban populations had consistently shorter FID than rural populations of the same species. A similar result was also found in dark-eyed junco in a recent urban colonization of San Diego, California; colonists were bolder and had reduced CORT responses when compared to wild populations (Atwell et al. 2012). Native birds were found to be more habituated than migrant birds in India, although there was evidence that migrant birds habituated throughout the day (Burger and Gochfeld 1991).

Yet, not all species adjust well to human disturbance, particularly those that have long FID, and rapid and strong corticosterone responses (Møller 2008). Carrete and Tella (2010) propose that individuals distribute themselves across the available environment according to their susceptibility to human disturbance, with more tolerant individuals occupying more highly disturbed areas (the "habitat selection" hypothesis). This has also been called "local site selection", and has been observed in black swans, *Cygnus atratus*, where genotypes associated with wary behavior were over three times more frequent at non-urban sites (van Dongen et al. 2015). In another study, chipmunks, *Tamias striatus*, distributed themselves in a non-random manner in response to human disturbance, with more explorative and docile chipmunks occupying more disturbed areas (Martin and Réale 2008). This means that shorter FIDs in urban areas may not be due entirely to habituation, but instead due to selective migration (or death) of susceptible individuals out of highly disturbed areas (Evans et al. 2010).

When the perceived risk is heightened or unpredictable (Knight and Miller 1996, Rodríguez-Prieto et al. 2010), sensitization occurs – or the increase of FID in response to a threat (Burger and Gochfeld 1981, Wheeler et al. 2009). For instance, wildlife species including vesper sparrows, (*Pooeceted gramieus*), western meadowlarks (*Sturnella neglecta*), American robins (*Turdus migratorius*), and mule deer (*Odocoileus hemionus*) showed greater responses to pedestrians hiking off-trail (unpredictable) vs. on-trail (predictable) (Knight and Miller 1996). In Dill's (1974a) experiment, zebra danios, *Brachydanio rerio*, with more predator experience had longer FIDs than fish with less experience. Marine iguanas, *Amblyrhynchus cristatus*, showed rapid sensitization (increased FID and CORT) as feral dog and cat populations increased on the Galapagos archipelago (Berger et al. 2007). A common situation where sensitization occurs is the hunting of game species (Fox and Madsen 1997). The hunting of water birds increased the FID of brent geese (*Branta bernicla*) by 160m in the span of one month (Smit and Visser 1993), and in flocks of pink-footed geese, *Anser brachyrhynchus*, FID increased by 100-200m during the shooting season (Madsen 1985). White-tailed deer (*Odocoileus virginianus*) maintained further distances from humans, and had increased FID and DF during the hunting season (Grau and Grau 1980). Higher levels of vigilance have also been observed in caribou (*Rangifer tarandus*) after the hunting season (Aastrup 2000). And in another study, FID varied between populations of roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) depending on the presence of hunting, with hunted populations having the highest FID (De Boer et al. 2004). Impala (*Aepyceros melampus*) located in hunting grounds have higher levels of vigilance behaviors compared to those located off hunting grounds (Matson et al. 2005).

6. Quantifying antipredator behavior: using predation-free simulated approaches

6.1 Prey responses to simulated approaches is comparable to that of predators

Because of the opportune nature of predation, it is often impractical to observe and sample real predation attempts due to infrequency and logistical complications. Instead, measures such as AD, FID, and DF are usually collected through simulated predation attempts using a stuffed or artificial model of a predator (Ekman 1987, Abrahams 1995, Jakobsson et al. 1995, Uchida et al. 2019), motorized vehicles (Burger 1998, Rodgers and Schwikert 2002, Mayer et al. 2019), or through approaches of a human experimenter (Stankowich and Coss 2006, van Dongen et al. 2015, Novčić and Parača 2022). Indeed, the first study to test FID used simulated approaches using a car, in 1934 testing interspecific differences in African ungulates FIDs (Hediger, cited by Walther 1969). Walther himself, in 1969, approached Thomson's gazelles (*Gazella thomsoni*) with a car to test whether FID depended on age, sex, and social status. Much of the literature on AD, FID, DF, and aggressive responses has been gathered using standardized experimental approaches, either with a human, a model predator, or a motorized vehicle. Although the real predation risk to a simulated predator is of course zero, the prey is initially unaware of this fact – and prey species are expected to have been selected to over-estimate rather than under-estimate risk, as the cost of under-estimating risk results in injuries or death (Frid and Dill 2002). Responses to human approachers are seen as a suitable proxy, as both approaches by a human and by a real predator result in the same behavioral responses (AD, FID, and DF), which divert time and energy from other fitness enhancing activities such as foraging, parental care, or territorial defense (Frid and Dill 2002, Beale and Monaghan 2004b).

The main difference between an approach by a human experimenter and that of a real predator is the numerical value of the FID, as FID is a result of calculations by the targeted prey about the perceived risk of the approach (Beale and Monaghan 2004b). A human approacher may be perceived as more or less risky than an approach by a real predator, as humans may provide an unknown or known level of risk to the targeted prey. If the human approacher is perceived as riskier, FID will be longer than for a real predator, or if the human approacher is perceived as less risky, FID will be shorter. But, this is only a concern if absolute values in response to a specific predator type are necessary for a study. In many studies, the objective is to compare responses among individual prey, making the relative threat of human approaches not problematic.

Some might argue that disturbance caused by a human experimenter cannot be comparable to a real predation attempt because many prey have evolved predator-specific antipredator behaviors (Frid and Dill 2002). However in measuring AD, FID, and DF in this manner, we are testing a response to a generalized threat and not predator specific responses (Frid and Dill 2002). In one example of this, zebra danio (*Brachydanio rerio*) were presented with the approach of real predator, a video of an approaching predator, or a video of a black dot that increases in size. All three approach types stimulated antipredator behaviors, and the resulting FID was affected by the size and speed of the approaching predator (or loom rate) (Dill 1974a, 1974b).

6.2 *The benefits of measuring antipredator behaviors (AD, FID, DF)*

The benefits of measuring antipredator behaviors are obvious. FID, in particular, is easy to simulate and measure: simply approach an animal and record the distance at which they initiate flight (Tarlow and Blumstein 2007). This can be done in a variety of contexts (environmental, social, reproductive) with relative ease. And, since the resulting measure is a distance, it is easy to standardize and compare across populations, species, and studies. However, AD in particular is often hard to observe in some animal species due to its lack of conspicuousness, and so starting distance is often used as a substitute (Blumstein 2003, 2010).

The one problem that must be considered when measuring FID is that the experimental Starting Distance (SD) has been commonly found to have a strong positive relationship FID, for example in 64 bird species out of 68 (Blumstein 2003). In Columbian black-tailed deer, starting distance had an impact on both AD and FID (Stankowich and Coss 2006), and the same was observed in a study covering a variety of bird species (Blumstein et al. 2005), and in several species of lizard (Cooper 2005, Cooper et al. 2009b), although this relationship is not observable in all species (Cooper 2005) and may be an artifact in some cases (Cooper 2008b). It is proposed that longer starting distances may increase monitoring costs and result in longer FIDs (Blumstein 2003), or alternatively that longer starting distances increase perceived predation risk (Cooper 2005, Cooper et al. 2009b). Hence, it is important to account for starting distance in all the analyses, or to choose a set starting distance from which to start all experimental approaches. One other thing to consider when analyzing AD and FID, is that mathematically $SD \geq AD \geq FID \geq 0$, always resulting in a positive linear relationship (although it is possible for the relationship to be weak and non-significant) (Dumont et al. 2012).

7. Scope and objective of the thesis

7.1 Antipredator behaviors in colonial seabirds: the case of the king penguin (Aptenodytes patagonicus)

In this thesis, the antipredator behaviors (AD, FID, DF, and aggression) of king penguins, *Aptenodytes patagonicus*, were explored by using standardized approach of a single human. King penguins are large, ground-laying, flightless seabirds that form extensive, densely packed colonies on sub-Antarctic shorelines (some containing over tens of thousands of birds, Barbraud et al. 2020). Breeding pairs incubate their single egg or young chick on top of their feet (Stonehouse 1960), which greatly reduces mobility. Successfully breeding king penguins take 14-16 months to raise a single egg to fledge (Stonehouse 1960, Weimerskirch et al. 1992), and therefore the reproductive investment in each offspring is extremely high. The eggs and young chicks are susceptible to high predation pressure from by giant petrels, *Macronectes halli* and *Macronectes giganteus,* and brown skuas, *Catharacta lonnbergi* (Hunter 1991, Descamps et al. 2005). These predators will harass incubating and brooding adults, sometimes causing them to flee and abandon their offspring. This puts strong selection on the antipredator behaviors of king penguins. Breeding adults have three decisions: (1) to stay and aggressively fight potential predators, risking fatal injuries, (2) to flee cumbersomely with the egg on top of their feet and cluster closer to neighboring breeders, or (3) to flee entirely, abandoning the current reproduction attempt in favor of own survival.

Breeding king penguins are highly aggressive, and actively defend their small breeding territory against both predators and conspecifics (Stonehouse 1960, Weimerskirch et al. 1992). Aggressive social interactions can average 100 interactions per hour (Côté 2000). Even when they are not directly implicated in social conflicts, king penguins are highly sensitive to social aggression, as demonstrated by elevated bystander heart rate responses to neighboring conflicts (Viblanc et al. 2012b). They also display elevated stress hormones and heart rates in more densely packed colony zones (Viblanc et al. 2014a, 2014b). While residing in a colony may help with predator detection (the many-eyes effect) and risk dilution, the social environment and frequent social aggressions may interfere with antipredator detection and flight.

As the colony does not only contain breeding birds, but also molting, non-reproductive, and courting birds, king penguins also provide the opportunity to explore antipredator responses over a diverse range of life history stages. It is possible to follow single individuals over longer periods of time, since breeding territories do not shift much during the reproductive period. Additionally, it is possible to compare the antipredator behaviors of breeders at different times of the reproductive cycle (i.e., early in incubation, early brooding, and late in brooding). After a lengthy incubation period of 54 days (Stonehouse 1960), chicks hatch in a semi-altricial state and remain highly dependent on their parents for feeding, protection, and body heat for the first 30 days of life. Aggressive territorial defense increases upon the hatching of the egg (Côté 2000), reflecting increased brood defense. Around 30 days old, chicks grow in a coat of down and gain thermal and physical independence although they continue to rely on their parents for food (Stonehouse 1960). These semi-independent chicks cluster into "creches", decreasing their risk of predation without needing protection from their parents (Stonehouse 1960, Le Bohec et al. 2005). Only adults that breed in the first half of the reproductive season (i.e., early breeders) are usually successful at fledging a chick, since late breeders are constrained by the arriving winter and hence their breeding success is virtually null (Van Heezik et al. 1994, Olsson 1996). Re-nesting potential is very low in this species, and therefore, the relative value of the brood should be higher for early breeding birds (Barash 1975, Andersson et al. 1980, Montgomerie and Weatherhead 1988, Redmond et al. 2009).

Finally, the island where this research is conducted (Possession Island in the Crozet Archipelago), hosts several king penguin colonies with varying levels of human disturbance. The colony where most research is conducted, "La Baie du Marin", is located next to permanent settlement, and scientific facilities are placed within the colony. Another colony, "Jardin Japonais", is located across the island and is only visited by humans several times a year.

7.2 Questions addressed in this thesis

This thesis investigates variation in antipredator behaviors (AD, FID, DF, and aggression) by utilizing standardized, predation-free human approaches to king penguins. Its aim is to explore antipredator behaviors in a variety of contexts and describe their occurrence in the king penguin. This thesis will answer questions that remain unaddressed in the literature by providing some unique analyses. By specifically focusing on the king penguin, I am able to explore environmental and intrinsic causes of variation in antipredator behaviors, as well as utilize the unique advantages that king penguin colonies provide (multiple life history stages present, the ability to follow an individual over time, and a complex and aggressive social system, see above).

7.2.a On repeatability, weather, and human disturbance

In Chapter 1, incubating king penguins are repeatably approached by a human experimenter. The main purpose of Chapter 1, is to test if antipredator responses are intrinsically determined by testing the repeatability of AD and FID. If AD or FID are repeatable, this is the first step in establishing personality in the king penguins (Réale et al. 2007, Dingemanse and Wright 2020), and also opens up further study of AD or FID in behavioral syndromes and coping styles (Sih et al. 2004a). In Chapter 1, I also take a first look at what causes variation in antipredator behaviors (AD and FID only). The first question that needs to be addressed is if the weather can affect antipredator behaviors, as controlling for the weather will always be a question for future analyses. I investigate temperature, and levels of sun, wind, and rain. Speed of approach will also be investigated as a factor that may affect AD and FID. From the literature, I know that faster speeds of approach frequently results in strongly increased FIDs (Cooper 1997, 2003b, 2006, Burger 1998, Cooper et al. 2003, 2009a, 2009b, Stankowich and Blumstein 2005, Stankowich and Coss 2006, Cooper and Whiting 2007, Bateman and Fleming 2011b, Samia et al. 2016). And finally, I compare AD and FID between two colonies, "La Baie du Marin" and "Jardin Japonais". These colonies differ in their level of human disturbance, and therefore we may be able to see sensitization or habituation in response to repeated human approaches.

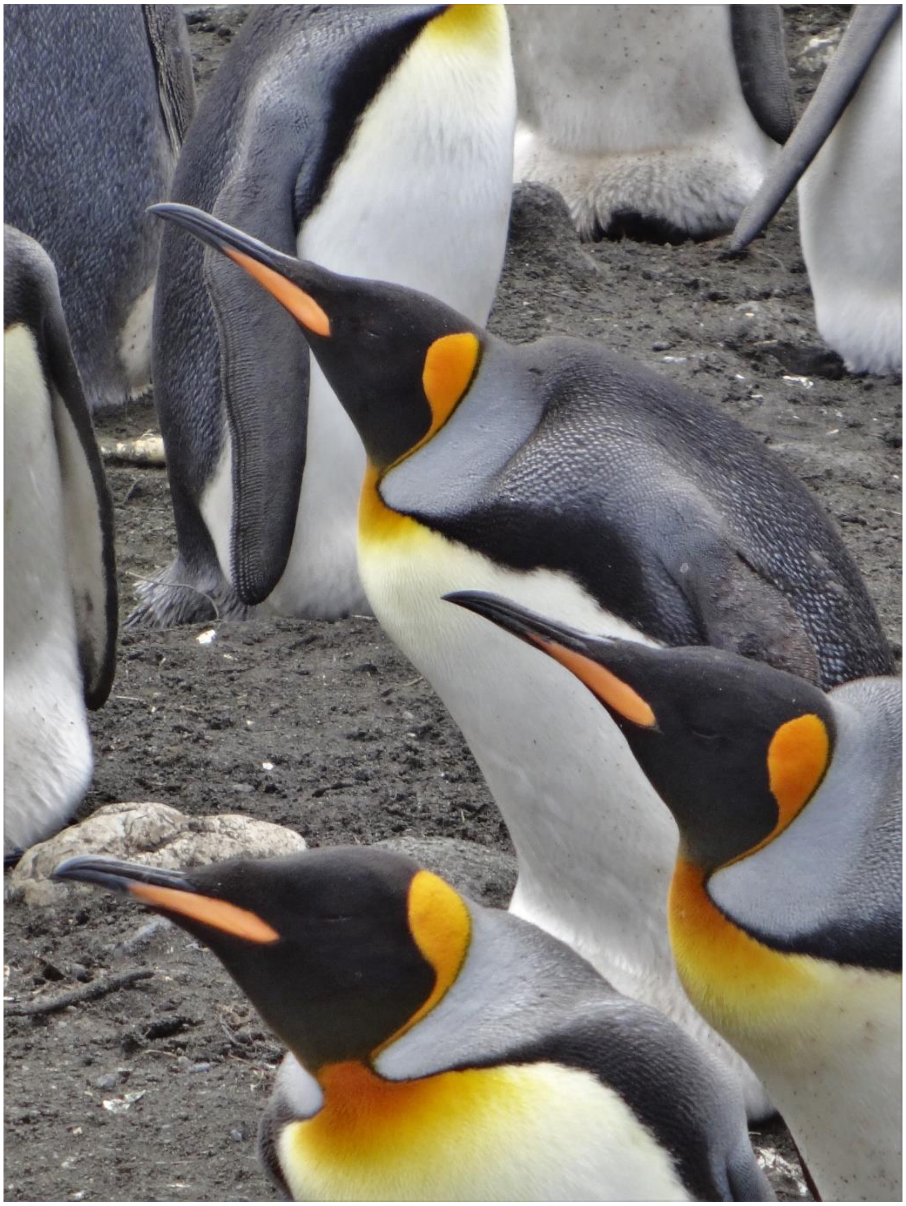
7.2.b The social environment

King penguins form colonies of thousands of birds on sub-Antarctic shorelines (Barbraud et al. 2020). Although these colonies are conspicuous and likely draw much attention from predators in the area, having so many neighbors may provide an advantage in earlier predator detection (more eyes are available to scan for predators at any given point, the "many-eyes" effect, Pulliam 1973; Caraco et al. 1980; Lima 1995), and predation risk dilution (Inman and Krebs 1987, Dehn 1990). Yet, king penguins are highly aggressive and spend much of their time within the colony engaged in territorial defense (Côté 2000). These frequent interactions may distract from detecting predators and engaging in antipredator behaviors (the distracted prey hypothesis, Chan et al. 2010). Finally, individuals on the outside of the colony likely face higher predation risk than positions inside the colony, as predators attack from the outside inwards (Jennings and Evans 1980, Burger and Gochfeld 1994, Morton et al. 1994, Reluga and Viscido 2005, Dias 2006, Fairbanks and Dobson 2007, Morrell et al. 2011). This leads to higher safety from predators in the center of the colony (selfish herd, Hamilton 1971). There may exist an edge effect (Pulliam 1973, Inglis and Lazarus 1981) in king penguin colonies, where individuals on the outside of the colony are more vigilant (and therefore have higher AD). In Chapter 2, I will test all four hypotheses (many eyes, risk dilution, selfish herd, and distracted prey) simultaneously to understand how the social environment might shape antipredator behaviors (AD, FID) in colonial seabirds. This is the first study to investigate all four hypotheses conjointly.

7.2.b Life history stage and the value of reproduction

In Chapter 3, I compare antipredator behaviors (AD, FID, DF, and aggression towards the approacher) across life history stages in the king penguin by using standardized human approaches, and test the hypothesis that breeding birds should be less prone to flee from approaching predators than non-breeders as the value of their current reproduction increases. Next, I test antipredator behaviors over the reproductive cycle (from incubation to egg hatching to chick thermal independence). Parents should increasingly choose to stay and defend their offspring as the egg/chick ages (as the brood continues to increase in value according to the brood value hypothesis), at least until the offspring can independently take part in anti-predator defenses. Finally, I test for differences in antipredator behaviors between early and late breeders. For a similar investment into reproduction, breeders with lower perspectives to fledge their young (i.e., late breeders) should invest less into offspring defense.

STUDY SPECIES, LOCATION, and METHODOLOGY



1. The king penguin (Aptenodytes patagonicus)

1.1 Life history and distribution

Penguins are a group of aquatic, flightless birds which inhabit the sub Antarctic and Antarctic regions of the southern hemisphere. Their wings (known as flippers) have lost the feathers of flight and have adapted for propelling the birds through water. They have distinctive counter shaded plumage with dark feathers dorsally and white feathers ventrally (Davis and Renner 1995, Williams 1995). Penguins spend most of their time at sea where foraging occurs, coming on land only to molt and breed. Therefore they possess numerous adaptations to deal with a dual life between land and cold water (waterproof and dense plumage, and fatty deposit layers) (Davis and Renner 1995, Williams 1995). While on land, all metabolism relies on reserves (mostly fat) accumulated during foraging trips at sea (Cherel et al. 1994a). Of the 18 currently defined penguin species (Vianna et al. 2020), the king penguin is the second largest, after the Emperor penguin (*A. fosterii*).

1. **Emperor penguin** – ***Aptenodytes forsteri***
2. **King penguin** – ***A. patagonicus***
3. **Gentoo penguin** – ***Pygoscelis papua***
4. **Chinstrap penguin** – ***P. antarcticus***
5. **Adelie penguin** – ***P. adeliae***
6. **Yellow-eyed penguin** – ***Megadyptes antipodes***
7. **Royal penguin** – ***Eudyptes schlegeli***
8. **Macaroni penguin** – ***E. chrysolophus***
9. **Snares penguin** – ***E. robustus***
10. **Fiordland penguin** – ***E. pachyrhynchus***
11. **Erect-crested penguin** – ***E. sclateri***
12. **Southern Rockhopper penguin** – ***E. chrysocome***
13. **Northern Rockhopper penguin** – ***E. moseleyi***
14. **Humbolt penguin** – ***Spheniscus humboldti***
15. **Magellanic penguin** – ***S. magellanicus***
16. **African (Jackass) penguin** – ***S. demersus***
17. **Galapagos penguin** – ***S. mendiculus***
18. **Little blue penguin** – ***Eudyptula minor***

Figure 7. The 18 currently known species of penguin. (Photo courtesy: Yves Handrich).

King penguins are found in sub Antarctic regions between 45 and 58°S and form breeding colonies on the northern areas of Antarctica and islands in South Georgia and in the South Indian Ocean (Stonehouse 1960). There are an estimated 1.1 million breeding pairs and the population overall is increasing (Birdlife International 2020). They are a long-live seabird that display high fidelity to their breeding colony (Olsson 1997, Descamps et al. 2009). Adult king penguins are 70-100 cm tall and weigh between 9-18 kg. Although males are slightly larger than females, both possess identical monomorphic conspicuous color ornaments, thought to play a role in sexual selection (Jouventin et al. 2008, Pincemy et al. 2009, Nolan et al. 2010, Dobson et al. 2011). These ornaments consist of an orange patch on the lower mandible, an auricular patch, as well as a chest patch that ranges from dark orange at the neck to yellow at the lower upper chest.

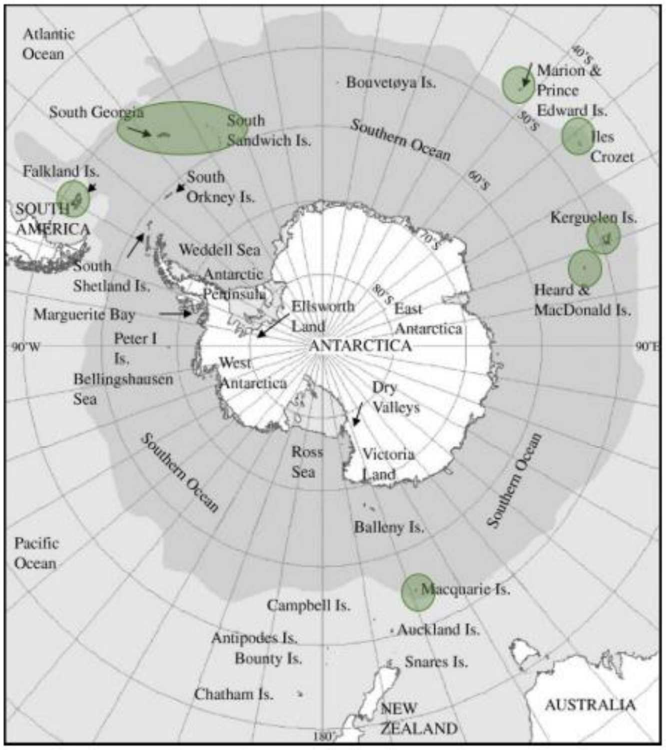


Figure 8. Map of the global distribution of king penguin colonies. The species consists of two subspecies, and each occupy a different geographic localization. *A. p. patagonicus* occurs in South Georgia, the Sandwich Islands, and the Falkland Islands. *A. p. halli* occurs in the Prince Edward and Marion, Crozet, Kerguelen, Heard, and Macquarie Islands (Davis and Renner 1995).

1.2 Foraging behavior and diet

When foraging during the daytime, king penguins make repeated dives over 100 m in depth, frequently diving past 300 m (Handrich et al. 1997, Pütz et al. 1998). Most dives take the form of a U-shape or W-shape, meaning that after a certain depth is reached, the bird then remains at the same depth for some time (often more than 5 minutes) while it forages (Pütz and Cherel 2005). Swim speed ranges from 1 m/s during the night to 2 m/s during the daytime (Shiomi et al. 2016). Feeding grounds vary for birds based in the Crozet Islands. In the austral summer (i.e., during the breeding season), birds swim southwards to forage at the polar front, some 400 km from their colonies. During the austral winter, when prey availability decreases, king penguins from Crozet travel further southwards to feeding grounds at the marginal ice zone, as far as 1600 km from the breeding colonies (Charrassin and Bost 2001, Pütz 2002). Myctophid fishes dominate the diet (chiefly *Electrona carlsbergi,* but including *Krefftichtys anderssoni, Protomyctophum tension* and *Protomyctophum choriodon,* they consist approximately 90% of the diet*)*, but also includes a gempylid (*Paradiplospinus gracilis*), paralepidids, nototheniids, channichthyids, squid and krill (Ridoux et al. 1988, Cherel and Ridoux 1992, Kooyman et al. 1992, Bost et al. 1997, Olsson and North 1997, Raclot et al. 1998, Cherel et al. 2002).

1.3 Breeding cycle

Although juvenile king penguins will attempt to breed upon their first return to the colony (Barrat 1976, Saraux et al. 2011), first successful breeding usually occurs around 5-6 years old (Weimerskirch et al. 1992). The breeding cycle of king penguins is long, complex, and energetically constraining; lasting 14-16 months from egg laying to chick fledging (Weimerskirch et al. 1992). King penguins are the only penguin species with a breeding cycle lasting longer than one year (Williams 1995). Prior to the start of the breeding season, in September, birds return to the colony for a prenuptial molt. During this time (a period of some 16-24 days), the birds fast on land, losing 58% of their body mass (Cherel et al. 1988, Descamps et al. 2002). Afterwards, they return to sea to forage for three weeks to restore their energy reserves before mating (Descamps et al. 2002). Mating begins with courtship rituals, wherein individuals give calls and exhibit their ornamentation, that result in the pairing off of individuals (Jouventin et al. 2008, Nolan et al. 2010, Dobson et al. 2011). Although apparently visually sexually monomorphic, vocal calls differ between sexes in their structure and frequencies (Jouventin 1982, Robisson 1992). During a reproductive cycle king penguins are monogamous; however, only about 20% of pairs breed again with the same partner in the following season (Olsson 1998). After courtship, the partners select a breeding territory within the colony (approximately 0.5 m^2, Côté 2000), which they defend from conspecifics and predators aggressively. Once established, breeding territories are highly stable and regularly spaced, and are strongly defended aggressively with a mean 100 aggressive interactions per bird per hour during incubation and brooding (Challet et al. 1994, Côté 2000). Once laid, the egg is about 10.6 cm x 7.4 cm and weighs on average 309 g. The egg is kept warm by resting on top of the parent's feet, and remaining in contact with a featherless patch of skin on the lower abdomen of the adult, termed the "brood pouch". The male and female partners alternate turns incubating the egg while the other partner returns to sea to forage, resulting in long periods of fasting for the on-shore individual (Stonehouse 1960, Weimerskirch et al. 1992, Descamps et al. 2002). Incubation shifts can last as long as 3 weeks but shorten as incubation progresses to a length of about 6 days or less when parents are feeding the young chick (Weimerskirch et al. 1992, Descamps et al. 2002). After the egg is laid, males usually take the first incubation shift while the female returns to sea, and incubation lasts for a total of 54 days (Stonehouse 1960). Hatching typically occurs in mid-January, and the chicks are hatched semi-altricial, with no feathers, and are reliant on their parents for food and warmth until about 20-40 days of age when a set of down feathers have grown in and they become thermally independent (Stonehouse 1960). Parents feed the chicks through regurgitated semi-digested meals of fish preserved for weeks by a beta-defensin antimicrobial peptide named "spheniscin" (Thouzeau et al. 2003, Landon et al. 2004). When chicks gain thermal independence, the parents spend longer and longer periods at sea foraging, leaving the chicks alone on land (Descamps et al. 2002). At this time, chicks group into large aggregations, called creches. These creches play an important role in antipredator defense through risk dilution, and as such there is evidence that chicks actively fight for the safest central positions (Le Bohec et al. 2005). At the start of winter, chick growth is interrupted (Stier et al. 2014), and chicks face their first long term fast, as prey availability declines and parents must travel further to forage (Charrassin and Bost 2001, Pütz 2002). Parents return infrequently and sporadically to their chicks over the winter period, leading to a 4 kg (or 68%) chick body mass loss over 5 months as chicks rely mainly on stored (fat) energy reserves during this time (Cherel and Le Maho 1985, Cherel et al. 1987, Saraux et al. 2012). Feeding restarts at the end of the subsequent spring, allowing chicks to finalize their growth and put on sufficient weight before fledging (Weimerskirch et al. 1986). Towards the beginning summer, chicks undergo a first molt to waterproof plumage (which strongly resembles adult plumage except for remarkably less coloration in the patches) after which they take to the sea and begin foraging on their own.

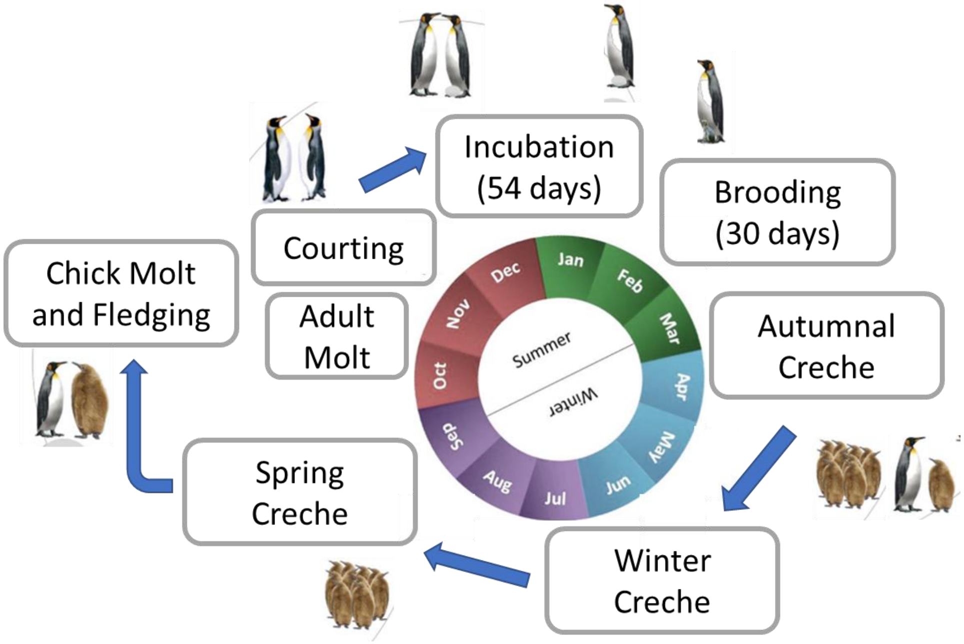


Figure 9. A schematic of the king penguin's yearly breeding cycle. This cycle represents the normal flow of events for an early breeding pair (i.e., one that did not successfully raise a chick the previous year). Adults undergo a pre-nuptial molt in spring (takes approximately 2-5 weeks), and then court and pair with a partner. The egg is laid in November and typically hatches mid-January after 54 days. The chick is hatched semi-altricial and is brooded for a further 30 days until it is able to move independently and has grown in a set of down feathers. During incubation and brooding, the adults take it in turn to incubate the egg and return to sea to forage. The downy chicks form into groups called creches, and adults spend much of their time during autumn at sea, but return regularly to feed their chick. During the winter, the adults remain at sea and rarely return to feed their chicks. Feeding is resumed in spring, at the end of which, the chick molts to water-proof plumage and is fledged.

Figure 10. Key phases of the reproductive cycle of a king penguin pair. King penguins display conspicuous courting behaviour in order to establish a pair. The pair then settles on a territory and begins to incubate their single egg. The egg hatches into a semi-altricial, featherless chick that requires from their parent body heat, food, and protection from predators. After 30 days, the chick grows in a coat of down and becomes mobile and thermally emancipated from their parent, although they still continue to rely on their parent for food. Emancipated chicks form creches in an effort to reduce predation risk. (Photo courtesy: first three, Quentin Schull. Last two, Tracey Hammer).

Initiation of incubation can begin anywhere from the beginning of November until the beginning of April. Because of the long breeding cycle (14-16 months), breeding occurs asynchronously (Weimerskirch et al. 1992, Olsson 1996). Normally it is unsuccessful breeders from the previous year who begin incubation first, in early November. Successful breeders necessarily begin the attempt to mate late the next year, as they fledge their chick in spring yet still need to undergo a pre-nuptial molt and replenish their energy stores before attempting to breed again in the subsequent year. (Weimerskirch et al. 1992, Van Heezik et al. 1994, Olsson 1996). This leads to a seasonally bimodal distribution of egg laying, with the first peak in November/December, and a second peak in February/March (Olsson 1996). These two distinct breeding strategies are termed “early” and “late” breeders. While early breeders face low breeding success (~30%), a late breeding attempt has virtually no chance of successful fledging of the chick (1%) as even successfully hatched chicks will not have critical stores of energy to last over the winter fast (Weimerskirch et al. 1992, Van Heezik et al. 1994, Olsson 1996, Stier et al. 2014). Because king penguins alternate between early and late breeding attempts, successful breeding only occurs every once in two or three years. It remains unclear why king penguins continue to choose late breeding as a strategy despite the low chance of successful reproduction.

The low success of late breeding implies that even for early breeding birds who lay and then lose their egg or young chick, a second attempt at reproduction within the same year will occur too late for successful breeding. This means that high reproductive value is placed on an early breeding attempt, and that the relative value of the offspring will increase as the offspring ages, such that chicks are worth considerably more than eggs (according to parental investment theory, Trivers 1972). This also means that for late breeding attempts, which are rarely successful, relative value of the offspring will be low, as will be parental investment. It has been found that late breeders devote the same proportion of time to comfort behavior and territorial defense as early breeders (Côté 2000, Viblanc 2011), however, it is unknown whether late breeders make similar decisions regarding offspring defense and predator avoidance behaviors as early breeders.

Sources of mortality for eggs and chicks are varied. For eggs, two of the main sources of mortality are predation by skuas or exposure to the elements (Hunter 1991). Young chicks face the same risks, but as they age they become targets of predation by giant petrels as well (Le Bohec et al. 2003, Descamps et al. 2005). Eggs and young chicks depend on their parents for protection from predators, and although adult birds are adapted to swiftly maneuver in the water, on-land, adults are ungainly in their movements which greatly increases the cost of flight (Pinshow et al. 1977). Not only is predation and exposure a risk for the young king penguin, but parents may also abandon reproduction if energy stores reach a serious level of depletion during a fast on land (Olsson 1997, Groscolas et al. 2000). One large source of mortality for chicks is starvation over the winter fast when parents return to land to feed their chicks rarely, if at all (Weimerskirch et al. 1992). Ultimately, breeding success is low (30%, Weimerskirch et al. 1992).

Key points to remember about the breeding cycle of king penguins are that: 1) parents on land rely solely on energy reserves that they accumulate during foraging excursions, 2) parents will fast for up to 3 weeks while waiting for their partners to return and relieve them, 3) the egg/young chick is kept on top of the parent's feet, in contact with the brood pouch, which greatly limits the mobility of the parent, 4) adults aggressively defend their breeding territories (around 1 m in diameter) from neighboring conspecifics and predators, 5) eggs and chicks are highly susceptible to predation, and 6) adult birds are adapted to swiftly maneuvering in water, not on-land, and so the energy costs of flight on land are high.

1.4 Predators

Although adult king penguins have an annual adult survival over 90% (Weimerskirch et al. 1992), king penguins face differing suites of predators on-land and at sea. Adult king penguins are much more vulnerable to predation at sea than on-land, being susceptible to predation from orcas, *Orcinus orca* (Condy et al. 1978) and fur seals, *Arctocephalus gazella*, (on land, Hofmeyr and Bester 1993; and at sea, Charbonnier et al. 2010).

Figure 11. At sea predators of king penguins. The first photo is of an orca, *Orcinus orca* (photo credit: rjdudley), and the second photo is of an Antarctic fur seal, *Arctocephalus gazella* (photo credit: D-Stanley).

On land, healthy adult king penguins are rarely the target of successful predation; however, the young (eggs and chicks) face strong predation pressure. Eggs and small chicks are predated on by brown skuas, *Catharacta lonnbergi*, kelp gulls, *Larus dominicanus,* and the scavenger snowy sheathbill, *Chionis minor* (Hunter 1991). Chicks, in particular, are the targets of giant petrels, *Macronectes giganteus* (southern giant petrel), and *Macronectes halli* (northern giant petrel) (Le Bohec et al. 2003, Descamps et al. 2005). Indeed, predation is the main cause of breeding failure for king penguins (Descamps et al. 2005).

Brown skua, also called Antarctic skua, subantarctic skua, southern great skua, or the southern skua, have a complicated and disputed taxonomy. They are sometimes subdivided into two or three species depending on the breeding location that they inhabit: the Falkland skua (*Stercorarius antarcticus*), Tristan skua (*Stercorarius hamiltoni*), and the subantarctic skua (*Stercorarius lonnbergi,* or, *Catharacta lonnbergi*) (Peter et al. 1990). They are the heaviest species of skua at 52-64 cm in length, 126-160 cm in wingspan, and a body mass of 1.4-2.15 kg (Peter et al. 1990). Inhabiting the sub-Antarctic region during summer when they breed, skuas are opportunistic predators (Trivelpiece et al. 1980, Peter et al. 1990, Hahn and Bauer 2008). When available, skuas will feed primarily on penguin eggs and chicks (Trivelpiece et al. 1980, Hahn and Bauer 2008), or scavenge carrion and placenta left by fur seals (Phillips et al. 2004, Anderson et al. 2009). During this time, skua breeding pairs hold feeding territories that they defend aggressively from intruders (Trivelpiece et al. 1980, Hahn and Bauer 2008). When their preferred food sources are unavailable skua will predate other seabirds and fish (Peter et al. 1990).

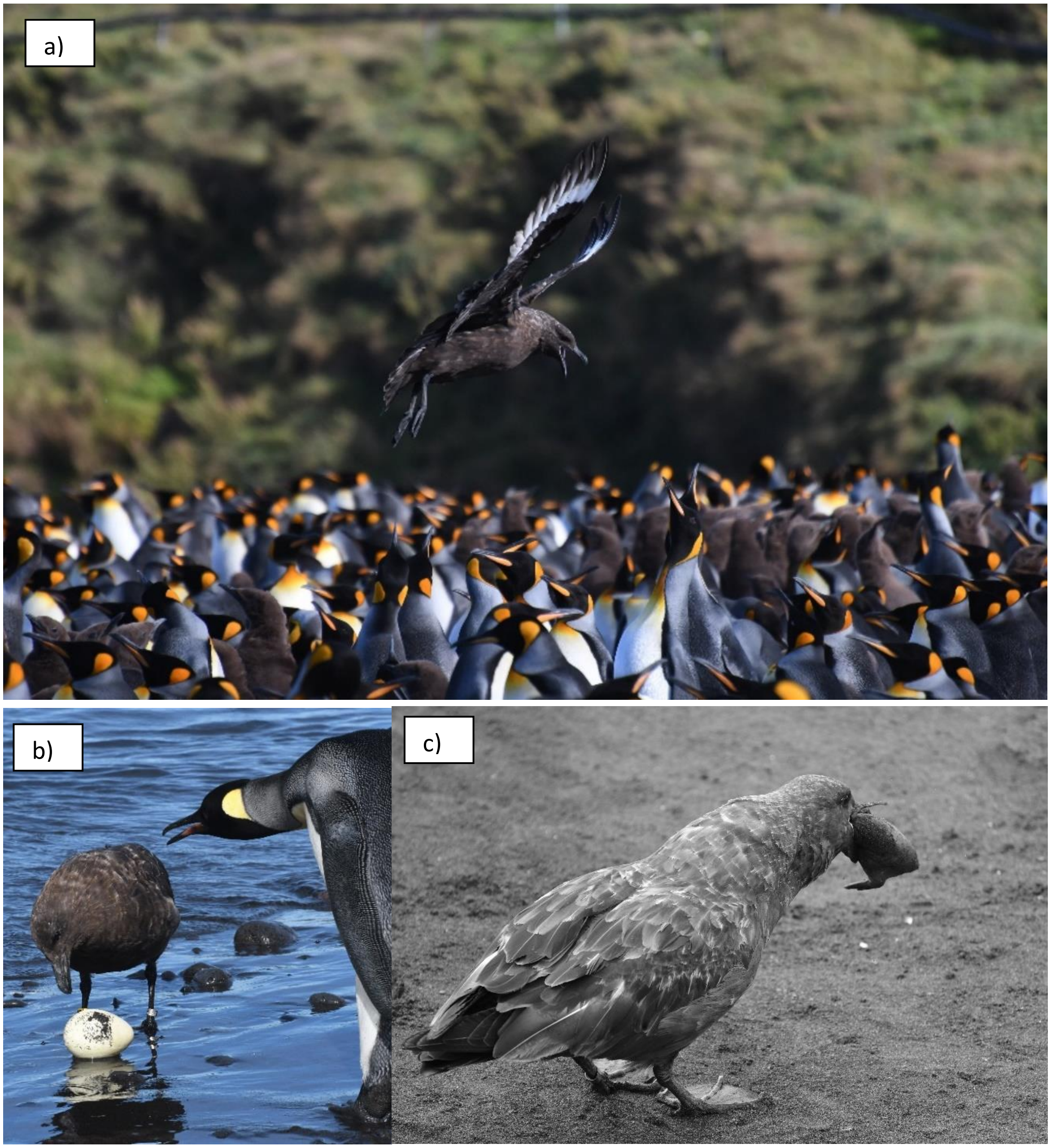


Figure 12. Brown skuas, *Catharacta lonnbergi,* as predators of king penguins. a) A brown skua scanning the penguin colony for unguarded eggs or chicks, b) a brown skua predating a successfully captured egg, and c) a brown skua with a young penguin chick. (photo credit: Manfred Enstipp).

Two species of giant petrel reside near the penguin colonies of interest to this study. These are the southern giant petrel, *Macronectes giganteus*, and the northern giant petrel, *Macronectes halli*. Their distribution overlaps to a large degree, from Antarctica to the subtropics of Chile, Africa, and Australia (Warham 1962, Conroy 1972, Patterson et al. 2008). Southern giant petrels are slightly larger, at 3-8 kg, 180-210 cm in wingspan, and 86-100 cm in body length (Warham 1962, Conroy 1972), while northern giant petrels are 3-5 kg, 150-210 cm wingspan, and 80-95 cm in body length (Warham 1962). The two species look remarkably alike and are hard to distinguish, as they both possess long, pale orange bills and mottled gray plumage, except for the rare white morph of the southern giant petrel. Giant petrels are scavengers as well as persistence predators that capture their prey through exhaustion and group mobbing; an attack by a giant petrel usually quickly attracts conspecifics to the predation site (Warham 1962, Conroy 1972, Hunter 1983). Once a targeted prey is exhausted, giant petrels use their sharply hooked bill to tear into the abdomen (Warham 1962). Giant petrels tend to feed first and preferentially on the entrails, but will also feed on meat and fatty tissue (Warham 1962). Giant petrels have a broad diet, but are known mainly as predators of penguins and scavengers of seal carrion (Warham 1962, Conroy 1972, Hunter 1983). When possible, giant petrels will feed on the placenta and dead pups of elephant seals, *Mirounga leonina* (Warham 1962, Conroy 1972). In the king penguin colonies (including the colonies of interest to this study), giant petrels predate mainly king penguin chicks, but are able to occasionally capture adults (Conroy 1972, Le Bohec et al. 2003, Descamps et al. 2005). Giant petrels are generally more active during the night (Le Bohec et al. 2003).

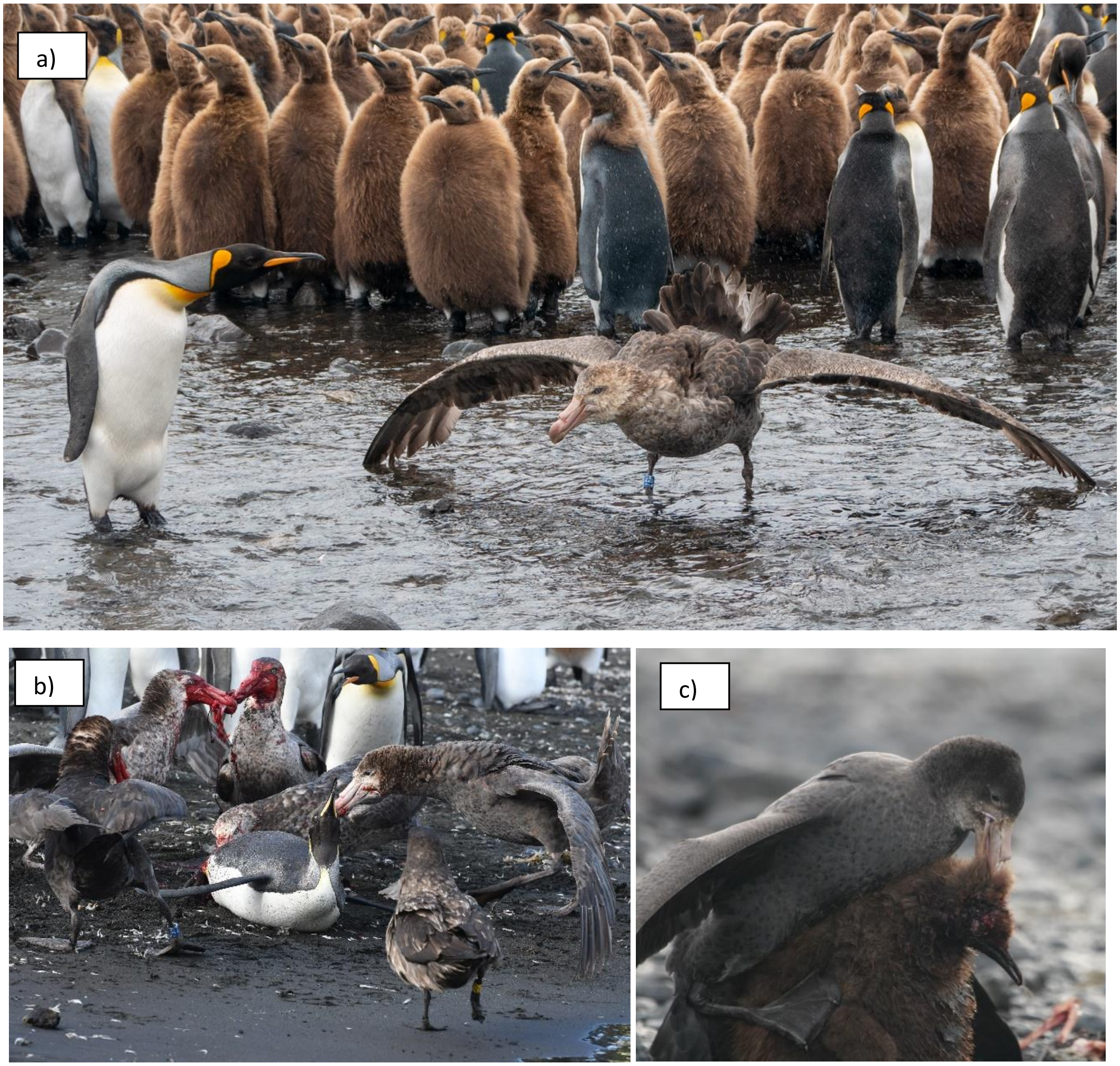


Figure 13. Giant petrels, either *Macronectes giganteus*, or *Macronectes halli,* as predators of king penguins. a) a giant petrel surveying the king penguin colony for susceptible individuals, b) giant petrels mobbing an adult king penguin prey, and c) a giant petrel capturing a king penguin chick using persistence and prey exhaustion. (photo credit: a, Camille Lemonnier; b, Manfred Enstipp; c, Aurélien Prudor).

2. Study site – The Crozet Islands

2.1. Geography

The Crozet Islands (*Îles Crozet,* 46°24'S, 51°45'E) are a sub-Antarctic archipelago of volcanic islands in the Southern Indian Ocean. They are a French owned set of islands, under the administration of the TAAF (Terres australes et antarctiques françaises, or the French Southern and Antarctic Lands). There are five islands, the two largest, which are of comparable size are East Island (130 km^2) and Possession island (150 km^2). The other three islands are Pig Island (67 km^2), Auk Island (3 km^2), and Apostle Islets (2 km^2). Possession Island is the only inhabited island, with a research station (Alfred Faure) located on the Eastern edge. This station houses some 30-50 personnel consisting of army, maintenance workers, and researchers. Visitors and staff are able to access the island only through the research vessel the Marion Dufresne (named after the French explorer who discovered the islands in 1772). The Crozet Archipelago hosts some 1 000 000 breeding pairs, which is more than half of the world’s entire population of king penguins (Guinet et al. 1995). This included the largest colony, located on Pig Island (Ile aux Cochons), which had an estimated 494 000 breeding pairs in 1988, (Guinet et al. 1995), but which has since declined by over 85% to 76 000 pairs by 2015 (Weimerskirch et al. 2018). Possession Island is home to 6 king penguin colonies of varying size: la Baie du Marin: 23 919 breeding pairs; Jardin Japonais: 25 793 breeding pairs; Petite Manchotière, 11, 213 breeding pairs; Cirque de la Chaloupe, 1311 breeding pairs; Mare aux Eléphants, 6458 breeding pairs; and Baie Americaine, unlisted colony size but smallest of the six) (Barbraud et al. 2020).

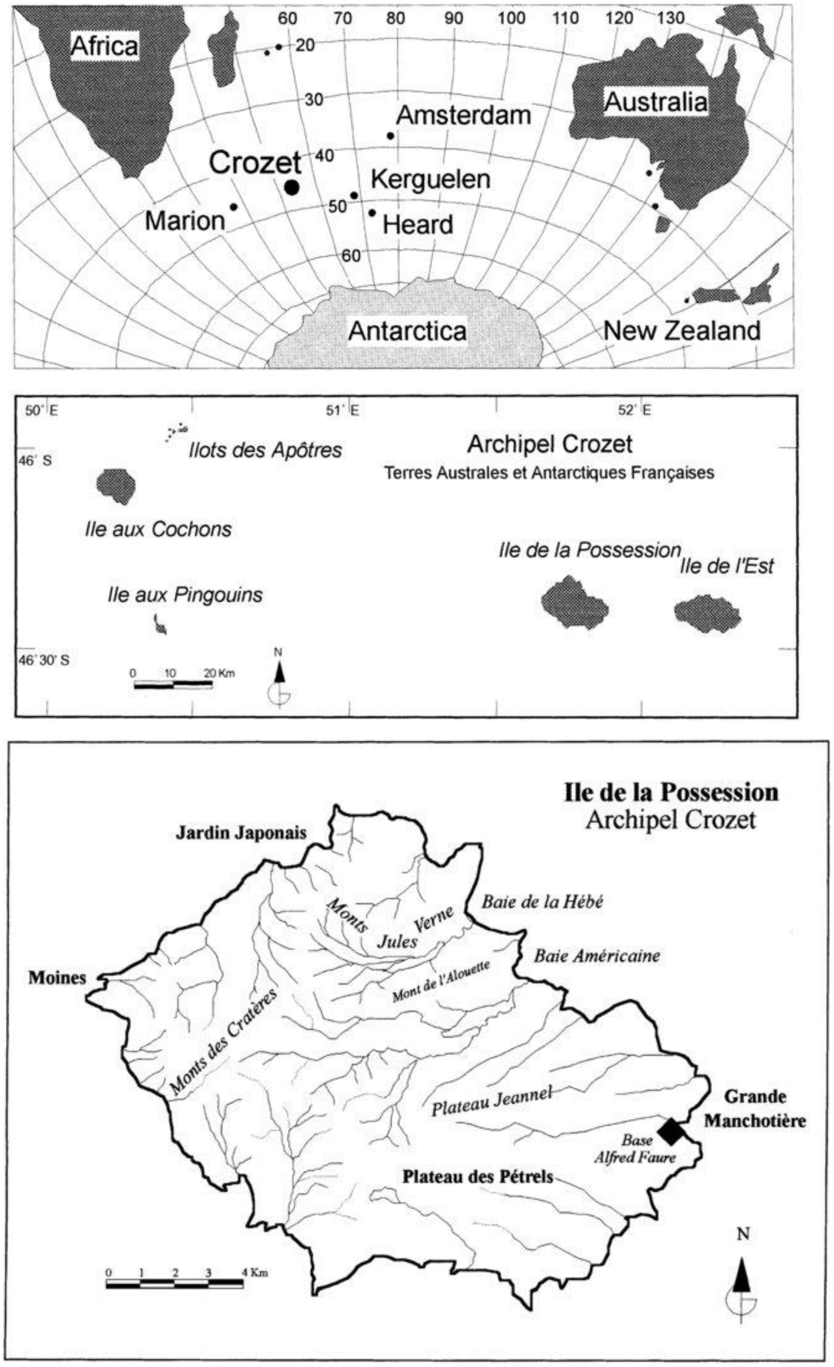


Figure 14. Location of the Crozet Islands in the Indian Ocean, map of the Crozet Archipelago, and map of Possession Island. Note the two main penguin colonies used in this study are labeled on the map of Possession Island: Grande Manchotière, now called “La Baie du Marin”, on the east side of the island, and “Jardin Japonais” on the north side of the island. The location of the research base, Alfred Faure is marked by the black diamond. (Reproduced from Vernon et al. 1997)

2.2. History

Originally discovered by the French explorer Marc-Joseph Marion du Fresne in 1772 (Mills 2003), the islands were regularly visited by sealer and whalers between 1804 and 1911 originating from France, Britain, and the United States (Headland 2018). Between 1924 and 1955, the islands were administered as a dependency of Madagascar. In 1938, the islands were declared a natural reserve, and by 1955 the islands became part of the French Southern Territories. In 1961, the research station was set up, becoming a permanent station by 1963. The research station specializes in meteorological, biological, and geological research and maintains a seismograph and geomagnetic observatory. In 2007, the Crozet Islands became a French Natural reserve where all research and visitation is limited except to those authorized by ministerial decree.

2.3. Climate

The Crozet Islands have a maritime-influenced tundra climate, with summer temperatures around 8°C and winter temperatures around 3°C, although temperatures can range from as high as 18°C and as low as -5°C. Precipitation is considerable, with over 2000 mm per year, and raining on average 300 days a year (Bougère and Bougère 1998). Wind levels are also high, with winds exceeding 100 km/h on a minimum of 100 days a year.

2.4. Flora and fauna

As a tundra-like, sub-Antarctic island, plant and animal life on the Crozet Islands are limited. Animals consist mainly of seabirds, seals, and penguins, while plants are limited to grasses, mosses and lichens (Duriez et al. 2005). Of the four species of penguin on the island, macaroni penguins are the most abundant (approximately 2 million pairs), but there are also substantial numbers of king penguins, as well as eastern rockhopper penguins, *Eudyptes filholi*, and gentoo penguins, *Pygoscelis papua* (Barbraud et al. 2020). There are 22 species of birds living on the islands, one is an endemic species of duck, the Eaton's pintail (*Anas eatoni*), and large populations of black-faced sheathbills (*Chionis minor*), brown skuas (*Catharacta lonnbergi*), southern and northern giant petrels (*Macronectes giganteus* and *Macronectes halli*), and six species of albatross (grey-headed albatross, *Diomedea chrysostoma*, yellow-nosed albatross, *Diomedea chlororhynchos,* Black-browed albatross, *Diomedea melanophris*, light-mantled sooty albatross, *Phoebetria palpebrata,* and the sooty albatross, *Phoebetria fusca*), including the wandering albatross (*Diomedea exulans*) (Weimerskirch et al. 1986). As for mammals living on the Crozet islands, there are fur seals, *Arctocephalus gazelle*, southern elephant seals, *Mirounga leonine*, and killer whales, *Orcinus orca,* which have been observed in the bays and waters near the islands. The introduction of foreign species has resulted in populations of mice, *Mus musculus,* and rats, *rattus* spp. forming on the Crozet islands. At one point there were also cats, *Felis catus,* pigs, *Sus domesticus,* and goats, *Capra hircus,* however all of these have since been removed. There are also several species of insects, such as wingless flies, and snails, and spiders. Fish surrounding the island are diverse, and include Patagonian toothfish, *Dissostichus eleginoides,* marbled rockcod, *Notothenis rossii*, and introduced species of trout.

2.5. This study

Our work was conducted mainly in “La Baie du Marin (BDM)” (46°25'S, 51°52'E), but some data was collected for Chapter 1 in “Jardin Japonais (JJ)” (46°21'S, 51°43'E). BDM is the most heavily researched colony on the island as it is located in close proximity to the research station Alfred Faure (1.5 km away, see Fig. 14). In BDM, scientific facilities are installed within the colony for researcher use and are shared between several different scientific programs. The research programs similarly share the colony of BDM, and our studies were conducted in the northern section of the colony, surrounded by the beach, river and road.

Data was collected for this study in 2010 - 2012, mainly during the austral summer months (November – April). I was personally present for data collection on the island during the austral summer of 2019-2020, though the data collected was purposed for the present thesis, but rather for a long-term study on the ecology, physiology, and behavior of these animals. A typical work day was very intensive, as a large variety of data was collected. Arrival at the colony occurred around 5:00 am, and at this time, locations and status of all tracked individuals were recorded. This took approximately an hour for two people to do. Afterwards, the bulk of the day was spent capturing and handling penguins. The handling of each bird took between 10 – 45 minutes depending on the procedure being carried out, and required two to three people per bird. During a typical capture, we recorded the social environment (density of near neighbors), structural size, body condition, parasite load, sampled blood, and deployed heart rate loggers and accelerometers. Longer handlings (45 minutes) occurred when we desired to record a stress response, which necessitated holding the birds for at least thirty minutes. In the late afternoon, when captures were complete, behavioral scans of followed birds were performed in each area of the colony, generally taking a further three hours or so to complete. Finally, after field work was finished for the day, one person prepared the blood samples and spent several hours in the lab running mitochondrial function tests using an Ouroboros.

Figure 15. Panoramic view of the king penguin colony at Baie du Marin. In the image, you can see the scientific installments in the center of the colony, as well as the dock used for boat visits. There is also a long, winding road which leads up the hill to the field station, Alfred Faure. (Photo credit: Onésime Prudhomme).

3. General methods

Although many different experiments were conducted in BDM over the years, a consistent method of bird approach including the measurement of AD and FID was implemented beginning in 2015. This means that, despite different experiments being conducted, birds were routinely approached in the same manner in order to record AD and FID for a study on these measures. Selection of the focal bird is initially random, but some focal birds were approached repeatedly over a period of several months as per the needs of the respective experiment. If individuals were to be approached multiple times, they were marked with non-permanent animal dye (Porcimark, Kruuse, Germany) on the chest for future identification from a distance. For some experiments the birds were followed since the start of incubation (often they were followed throughout reproduction), allowing for the knowledge of sex and incubation status and stage, but this was not the case for all experiments. Mainly incubating, and sometimes brooding, birds were used in the experiments, but this was not always the case (for example, in Chapter 3, a wide range of reproductive status were included). Birds were also microchipped at the end of most experiments, allowing us to know about previous exposure to humans for some birds. For this study, we used only birds with no previous history of human disturbance. All approaches occurred between 5:00 and 19:00.

3.1. Approach protocol

Before a bird was approached, several measures were taken out of eye-sight of the focal bird. Weather variables were recorded; sometimes air temperature (°C), but not always. Sun, rain, and wind were scored on a scale of 0 to 2, with a score of 0 denoting no wind/rain, or full cloud (i.e., no sun), and a score of 2 denoting full, heavy, or strong. Next, the number of neighbors in the nearest circle around the focal bird were recorded, as were the minimum and maximum, or mean distances of the focal bird to its neighbors (see Fig. 16). Finally, the starting distance was recorded, since this has a known effect on FID (Blumstein 2003, Dumont et al. 2012).

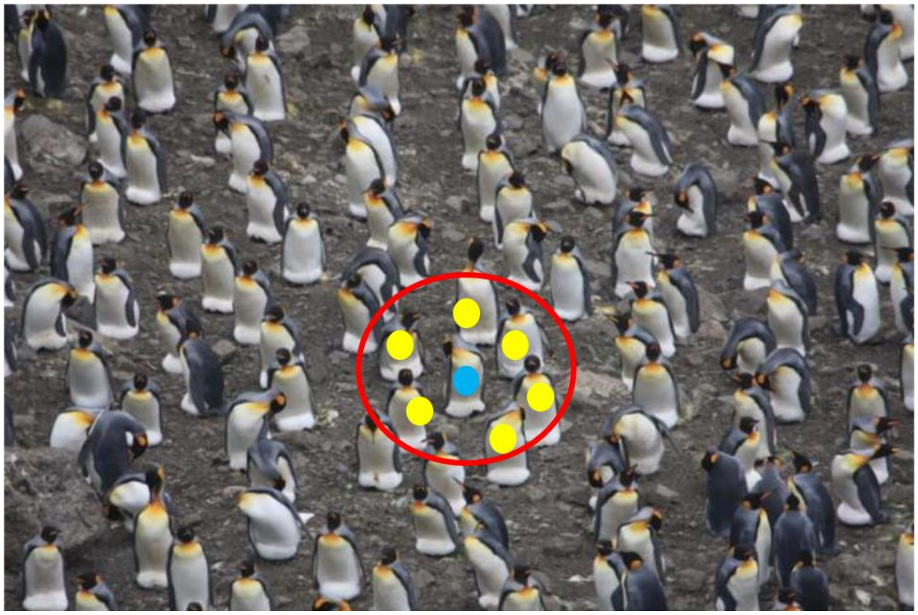


Figure 16. Identifying the number of neighbors. The focal bird is denoted by the blue circle, and the nearest neighbours are marked with yellow circles.

Birds were approached at a regular pace following a direct trajectory towards the focal individual and in plain line of site. Distances between the approaching experimenter and the focal bird were measured at alert (AD, the bird tilting or stretching its neck in the direction of the experimenter) and at flight initiation (FID, the bird attempting to walk away from the experimenter, with their egg on top of their feet for incubating birds). Speeds of approach were also measured, another variable known to strongly correlate with FID (Stankowich and Blumstein 2005, Cooper and Whiting 2007, Bateman and Fleming 2011b).

Chapter 1

Repeatability of alert and flight initiation distance in king penguins: effects of colony, approach speed and weather

Tracey L Hammer[1], Pierre Bize[2], Claire Saraux[1], Benoit Gineste[1,3], Jean-Patrice Robin[1], René Groscolas[1]

and Vincent A Viblanc[1]

[1]University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000 Strasbourg, France

[2]School of Biological Sciences, University of Aberdeen, AB24 2TZ, UK

[3]IPEV – Institut Polaire Français Paul Émile Victor, 29280 Plouzané, France

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ABSTRACT

Alert Distance (AD) and Flight Initiation Distance (FID) are popular measures used to explore the reaction of prey to approaching predators, and thus the economics that underlie optimal escape strategies. AD likely mirrors the effort invested into vigilance, while FID provides an estimate of the perceived risk of an approaching threat. Although individual variation in AD and FID is influenced by environmental factors such as variation in predation pressure and human disturbance, the repeatabilities of these traits (especially AD), and therefore their designation as a personality trait, remain under investigated. Here, we studied the repeatability of AD, FID, and the decision to flee in a flightless, ground-breeding seabird, the king penguin (*Aptenodytes patagonicus*). A single experimenter approached three times over three consecutive days 47 incubating king penguins from two different colonies with varying human disturbance levels. We explored the effects of weather, time of day, and approach speed of the experimenter on these behaviors. Weather had an effect on all three behaviors. In warm, sunny weather AD increased, while in rainy, windy weather birds were more likely to flee yet waited longer before initiating flight. Faster approach speeds between AD and FID increased FID. Weather conditions and speed of approach affected repeatability estimates, highlighting the need to consider external sources of variation when refining such estimates. FID and the decision to flee were significantly and moderately repeatable (r = 0.26 and 0.57 respectively), while AD was not. There was no evidence of habituation or sensitization due to colony.

Key words: *Aptenodytes patagonicus*, personality, human disturbance, optimal escape decisions, predation risk,

INTRODUCTION

Understanding how wild animals react to threats - especially predators - and the economics underlying (optimal) escape decisions, is a central topic in behavioral ecology that has been widely studied by evaluating Alert (AD) and Flight Initiation (FID) Distances (Tätte et al., 2018; Blumstein, 2019; reviewed in Frid & Dill, 2002). AD and FID can be defined as the distances at which a focal animal interrupts its normal behaviour to become alert (AD) or begin to flee (FID) from an approaching predator. AD provides us with a surrogate of the amount of time, and possibly energy, invested by the focal individual into surveying its surrounding; i.e., the degree of vigilance (Fernández-Juricic and Schroeder, 2003; Beauchamp, 2015; Uchida et al., 2019; but see Tätte et al., 2019). Meanwhile, variation in FID informs us on the perceived predation-risk of the focal individual (Blumstein, 2006, 2019; Møller et al., 2008).

In practice, the decisions that prey undertake when approached by a predator (AD and FID) can be simulated by performing non-lethal approaches by human experimenters (Frid and Dill, 2002; Beale and Monaghan, 2004a). Animals are expected to respond in much the same way to human approach stimuli as they would to actual predators since (1) both divert time and energy that could be otherwise invested in fitness enhancing activities; and (2) animals should be selected to overestimate rather than underestimate risk due to the cost of miscalculation, *i.e.*, injury or death (Frid and Dill, 2002). While AD can be hard to observe in some species or contexts, FID has the advantage of being easily measured and quantified (Tarlow and Blumstein, 2007). Both can be standardized within and across studies (Blumstein, 2006; Møller et al., 2008), and are species-specific (Blumstein et al., 2003; Møller, 2008; Carette and Tella, 2011; Piratelli et al., 2015). As a consequence, FID in particular and AD when available, have become popular measures in conservation biology used in establishing set-back distances and buffer zones to minimize stress-related disturbances on wildlife (Rodgers and Schwikert, 2002; Fernández-Juricic et al., 2005).

Although AD and FID are species-specific, there is fast accumulating evidence that FID (and to a lesser extent AD) can vary among populations of the same species and between individuals within the same populations (Edwards et al., 2013). For instance, FID is often shorter in urban versus rural populations (Piratelli et al., 2015; Carette and Tella, 2017), suggesting either that these animals have habituated (or developed tolerance) to human disturbance (Burger and Gochfeld, 1981, 1990; Walker et al., 2006), or that less tolerant individuals have migrated away from human presence (Ellenberg et al., 2009; Carette and Tella, 2010, 2011). Further, upon repeated approaches, FID has been shown either to decrease (habituation: Carter et al., 2012; Petelle et al., 2013; Arroyo et al., 2017), or increase (sensitization: Dill, 1974; Wheeler et al., 2009), demonstrating within-individual plasticity. FID can display consistent inter-individual (repeatable) variation over time (Carette and Tella, 2010; Carter et al., 2012; van Dongen et al., 2015). The same cannot be said of AD, which remains to be explored; however, vigilance behavior has often been found to be mildly repeatable (Couchoux and Cresswell, 2012; Roche and Brown, 2013). Repeatable behavioral traits measured over time are a prerequisite for the characterization of individual personality or temperament traits (Dingemanse & Wright, 2020), and might suggest genetic or early environmental constraints shaping individual risk-taking behavior. In fact, due to its repeatability, FID is frequently used as a metric to explore boldness (Atwell et al., 2012; Petelle et al., 2013; Highcock and Carter, 2014; Young et al., 2015), one of the five main personality traits defined by Réale et al., (2007), which is associated with risk-assessment and risk-taking, particularly in the context of predation and disturbance.

AD and FID should be strongly selected in prey species, in a way that balances the survival benefits of escaping approaching predators with the costs of abandonning other fitness-enhancing activities such as reproduction (Ydenberg and Dill, 1986). Consequently FID is known to vary with the perceived risk of predator approaches (Frid and Dill, 2002; reviewed in Stankowich and Blumstein, 2005) including the size or number of predators (Beale and Monaghan, 2004a; Geist et al., 2005), directness of approach (Smith-

Castro and Rodewald, 2010; Sreekar and Quader, 2013; but see Fernández-Juricic et al., 2005), speed of approach (Bateman and Fleming, 2011; Samia et al., 2016; but see Lafferty, 2001), and predator intent (*i.e.*, predator suddenly turning towards the prey or maintaining a purposeful gaze; Cooper, 2003; Bateman and Fleming, 2011; Sreekar and Quader, 2013). FID has also been shown to vary with the time of day (Patelle et al., 2013; Piratelli et al., 2015, Ferguson et al., 2019), can be reduced when prey have low energy reserves (Beale and Monaghan, 2004b; Piratelli et al., 2015), are in a large group (dilution effect; Ydenberg and Dill, 1986; Burger and Gochfeld, 1991, Santoyo-Brito et al., 2020), or are in close proximity to refuge (Cooper and Whiting, 2007). AD has not been explored to the same extent as FID, but evidence suggests that vigilance behaviour is also modified by time of day (Edwards et al., 2013), weather conditions (Couchoux and Cresswell, 2012), conspecific interactions (Hess et al., 2016), sex and reproductive status (Burger and Gochfeld, 1994), and group size (Díaz and Asensio, 1991; Carter et al., 2009; Boujja-Miljour et al., 2018).

The cost-benefit fitness trade-off of fleeing a tentative predator should be particularly strong for ground-laying birds tied to vulnerable nesting sites, such as penguins. Penguins commit a high amount of time and energy to reproduction (obligate bi-parental care, long-term fasting, prolonged breeding cycle and chick development; Williams, 1995), and face a strong fitness trade-off between the survival costs of defending their brood against predators (*i.e.,* injuries and potential death for the adult) and the reproductive costs of abandoning their current reproduction but surviving to breed another year (Montgomerie and Weatherhead, 1988; Frid and Dill, 2002; Dowling and Bonier, 2018). Accordingly, penguins are usually highly territorial and defensive of their brood (Viñuela et al., 1995; Amat et al., 1996; Côté, 2000), though within species there is clear variation on the degree of territoriality and aggression depending on brood value (Amat et al., 1996; Côté, 2000), the type of threat considered (Lee et al., 2017), and bird personality (Traisnel & Pichegru, 2018). Surprisingly, few studies have investigated how variable AD and FID to approaching predators are in penguins, nor the factors affecting those traits, despite their importance in shaping breeding decisions, and despite the fact that several studies have documented marked effects of disturbance (e.g. ecotourism) on penguin behavior (vigilance and locomotory behavior, time budgets; Holmes et al., 2005, 2006; Burger and Gochfeld, 2007), physiological stress (Ellenberg et al., 2006, 2012, 2013; Viblanc et al., 2012; Carroll et al., 2016), or reproduction (Giese, 1996; McClung et al., 2004; Ellenberg et al., 2006; reviewed in Bateman and Fleming, 2017).

Here, we investigated the variability of both AD and FID in breeding king penguins (*Aptenodytes patagonicus*). King penguins are large, ground-laying, flightless birds that form extensive colonies on the subantarctic shorelines. Breeding pairs incubate their single egg or young chick on top of their feet (Stonehouse, 1960), therefore limiting their mobility. They are subject to on-land predation mostly by giant petrels, *Macronectes halli* and *Macronectes giganteus*, and brown skuas, *Catharacta lonnbergi* (Hunter, 1991; Descamps et al., 2005). Giant petrels and skuas especially target eggs and chicks, but petrels are also known to prey on injured adults (Hunter, 1991). These predators will harass incubating and brooding adults sometimes causing them to flee and abandon their eggs. Breeding adults have three choices: first to stay and fight, risking potentially fatal injuries; second to flee slowly cumbersomely with the egg on top of their feet clustering closer to neighbouring breeders; or finally, to flee entirely, guaranteeing survival but abandoning their current reproduction.

We calculated individual repeatabilities for AD and FID which were measured several times on incubating adults, and assessed the potential influences of approach speed, weather conditions, and time of day on AD and FID as these may impact the levels of vigilance and responsiveness to a threat. Specifically, we expected AD and FID to vary in a quadratic function, increasing at dawn and dusk, and coinciding with highest predation risk for chicks (giant petrel activity is highest at early and late hours of the night; Le Bohec et al., 2003; Descamps et al., 2005). We further tested whether individuals sensitized or habituated to repeated approaches by a human experimenter by examining bird responses in two different colonies; one close to human settlements and one relatively unexposed to human disturbance.

King penguins have been shown to express significantly lower heart rate stress responses to human approaches in disturbed areas vs. undisturbed colony areas (Viblanc et al., 2012). Thus, we expected individuals measured in the colony close to human settlements to show habituation to approaching experimenters (decreased AD and FID compared to the undisturbed colony).

METHODS

Study sites

This study was conducted in mid-to-late January during the Austral summer of 2010-2011. Birds were selected from two colonies of king penguins located on Possession Island in the Crozet Archipelago, namely the colonies “La Baie du Marin” (BDM, 46°25’S – 51°52’E) and “Jardin Japonais" (JJ, 46°21’S – 51°43’E). BDM is home to ca. 22 000 breeding pairs (Barbraud et al., 2020) and is located on the east side of Possession Island in close proximity to a permanently inhabited research station built in 1961. This colony has been exposed throughout the year for the past 50 years to the daily presence of scientists and non-scientists in or close to the colony (Viblanc et al., 2012). During this time, birds in BDM have been regularly exposed to humans including tourist visits, censuses, population counts, and systematic monitoring. Meanwhile, JJ is home to ca. 39 000 breeding pairs (Barbraud et al., 2020) and is located on the north side of the island some 13 km from BDM. JJ is a relatively undisturbed colony, far from the research station and visited by scientists only a few times every year for population count and census information.

Approach protocol

We repeatedly approached a total of 47 incubating birds in the two colonies (23 birds from JJ and 24 birds in BDM). Each individual was approached once per day over three consecutive days between the hours of 8:00 and 19:00 (from Jan. 11 - 13 in JJ, and from Jan. 30 - Feb. 1 in BDM). It was not possible to find all birds on the subsequent days and so two birds in BDM were only approached once, and one bird each in JJ and BDM were only approached twice. Following egg-laying, king penguin partners alternate incubation duties, allowing their partner to forage at sea while they fast on land (Stonehouse, 1960). The male takes the first incubation shift, and the egg hatches some 53 days later, usually during shift four when the female has possession of the egg (Weimerskirch et al., 1992).

Following the STRANGE guidelines (Webster & Rutz 2020), we provide hereafter details on how incubating birds were selected and highlight potential biases related to the selection of our study subjects. Birds were selected haphazardly while incubating their eggs, and therefore we had no individual information on their sex, age, incubation shift, or previous experience with humans. Chosen individuals visually appeared in good physical condition, based on their plumage (shiny) and morphological (fat) appearance, and thus had not been fasting for extended periods of time. Individuals were selected at distance, and not after being approached or captured. Therefore, we expected no strong initial sampling bias in relation to how individuals were responding to human approaches (but see discussion).

Selected individuals were marked from a distance (roughly 1 m) at the end of the first approach using a dot of non-permanent pressurized spray animal dye (Porcimark®, Kruuse, Lageskov; Denmark) on the belly for identification during subsequent approaches. All approaches were performed by the same observer (BG) dressed in the same clothing. Individuals were only approached if they were resting upon arrival of the observer (*i.e.*, not engaged in aggressive, preening, or sleeping behaviours). The approach started after having observed the bird resting for at least one full minute before approaching it. During this time, the experimenter hid out of line of sight. Each approach had a set starting distance of 18 m, as measured with a laser telemeter (Leica DISTO^{TM} D5 Lasermeter, Leica Geosystems AG, Hexagon, Sweden), which we standardized due to the known influence of starting distance on FID (Blumstein, 2003, 2010; Dumont et al., 2012). We chose a starting distance of 18 m based on preliminary observations of 59 king penguins, including courting (paired) and incubating birds (a sample representative of the various life-history stages in the colony, excluding moulting and chick-brooding birds), that showed the maximal distance at which birds exhibited signs of vigilance towards an experimenter was 12.45 m and the minimal distance was 3.03 m (mean ± SD = 6.85 ± 1.87 m). We used a starting distance 1.5 times greater than the maximal detection distance recorded in the preliminary study to ensure starting distance far exceeded maximum alert distance (see also Fleming and Bateman, 2017).

The approaching observer followed a direct trajectory toward the focal individual, in plain line of sight, always starting from outside the colony. The experimenter walked until the first sign of alert was detected (the bird tilting its head or stretching its neck in the direction of the experimenter). At this distance, termed the Alert Distance (AD), the experimenter took a standardized one-minute pause to record AD and time. The time from the start of the approach until the bird became vigilant was recorded with a stopwatch and the remaining distance to the selected bird measured with a laser telemeter (closest cm). The approach was then resumed until the bird showed the first signs of fleeing (slowly walking away with its egg resting on its feet) – termed Flight Initiation Distance, FID. Some birds never showed signs of flight while being approached, right up until close (FID = 0 m) (see also Bateman and Fleming, 2011, for similar results in ibises). FID had therefore a zero-inflated distribution (see supporting information S1), suggesting this measure reflected two different processes: *i*) the decision to flee or not (0/1); and *ii*) the distance at which flight (escape) should occur if birds decide to flee. Hereafter, we analysed these two processes separately. We calculated the speed of approach (m/s) prior to the occurrence of AD and FID as the distance walked (m) divided by the duration of approach (s). The mean speed ± SE of approach prior to AD was 0.61 ± 0.09 m/s (range = 0.44 – 0.86 m/sec) and the mean ± SE speed of approach between AD and FID was 0.57 ± 0.10 m/s (range = 0.35 – 0.90 m/s). Walking speed varied slightly due to topography, entering the colony, and breeder density.

At the start of each approach, we recorded air temperature to the nearest 1°C, and we scored wind speed, solar levels, and rain on a scale from 0 to 2, with half levels (i.e., 0.5) being allowed. A value of 0 indicated no wind or rain, or full cloud cover (no sun). A value of 2 indicated heavy wind or rain or full sun. Mean temperature was 10 °C (range = 7 – 13 °C). As air temperature, wind speed, rain, and solar levels were naturally correlated, we used a Principal Components Analysis (PCA) to summarize all weather variables (package "FactoMineR", Lê et al., 2008). This approach had the advantage of capturing climatic variation on a continuous scale through two independent and orthogonal axes, and avoided strong collinearity (VIFs >30) issues if 'raw' meteorological variables are used in the analyses. We kept the first two principal component (PC1 and PC2) which together explained over 84% of the variation in climate data. Increasing PC1 (64.86% of variation) values were mainly associated with higher sun scores (correlation = +0.939) and higher temperature (+0.918), and to a lesser extent higher wind scores (+0.639), and lower rain scores (-0.686). In contrast, increasing PC2 (19.77% of variation) values were mainly associated with higher wind scores (+0.702), higher rain scores (+0.543), but not with sun scores (-0.010) or temperature (-0.061). Thus, increasing PC1 values described sunnier, warmer days while increasing PC2 values described windier, rainier days. On average, the climate conditions varied during our three approaches in both colonies (see supporting information S2), highlighting the need to control for climatic variation in further analyses.

Statistical analyses

All statistical analyses were performed in R 3.6.1. (R Development Core Team, 2020). Results are presented as means ± SE. We investigated the sources of variation in AD (gaussian distribution), the decision to flee or not (FID: 0/1, binomial distribution), and the distance at which flight was taken for birds that did decide to flee (FID > 0; gaussian distribution) using linear mixed models (LMM) and generalized linear mixed models (GLMM) with the appropriate error distribution. In all the models, we entered individual ID as a random factor to control for repeated measures, and we included as fixed effects the time of day, weather (PC1 and PC2), approach speed, approach order (three levels: first, second, or third approach), and the colony (two levels: BDM vs JJ). To test whether birds differed in their behavior at different times of day, and whether habituation or sensitisation to human approaches occurred differently between colonies, we also included second order interaction *colony* x *approach order* and *time of day x time of day* (viz., time^2) in our starting models. Second order interactions were dropped from the final model if not significant. Models were run using the *lmer* and *glmer* functions in the package "lme4" (Bates et al., 2015). The significance of the fixed effects was tested with the *anova* function (type 3) from the package "lmerTest" (Kuznetsova et al., 2017) using F tests with Satterthwaite estimation for the denominator degree of freedom for models with a gaussian distribution. Pseudo-R^2 for the models were calculated using methods developed in Nakagawa and Schielzeth (2013). Prior to analysis, time of approach was converted to decimal time, and non-zero FIDs were log-transformed (natural log) to normalize the distribution of the residuals. Independent variables were checked for collinearity using Variance Inflation Factors (VIF) (Zuur et al., 2010). A few VIFs were above 3 (see results), but those were considered acceptable as they represented different categorical levels of the same factor (*e.g.* approach order). All variables were scaled and centered prior to inclusion in the models to compare effect sizes (Schielzeth, 2010). Where appropriate, we insured model residuals were normally distributed by visual inspection of density distributions, Q-Q plots, cumulative distribution functions, and P-P plots using the "fitdistrplus" package in R (Delignette-Muller and Dutang, 2015).

Repeatabilities and their confidence intervals were calculated using the functions *rpt* for AD, and FID and *rptBinary* for the decision to flee or not, from the "rptR" package in R (Stoffel et al., 2017). Repeatability was calculated as the ratio of among-individual variance in AD or FID (σ^2_α) over total phenotypic variance (equal to the sum of among-individual variance and within-individual variance, σ^2_ε), so $r = \sigma^2_\alpha / (\sigma^2_\alpha + \sigma^2_\varepsilon)$ (Nakagawa and Schielzeth, 2010). We first calculated agreement repeatability, also called uncorrected repeatability, *r*, which is simply based on the among- and within-individual variance in AD or FID. Afterwards, significant effects from the above models, which influenced the expression of AD and FID, were controlled for when calculating adjusted repeatability r_{adj}, (also called corrected repeatability) (Wilson, 2018).

Ethics statement

No animal was caught or handled over the course of this study. The research was approved by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor. Authorization to enter the colony and approach birds was obtained from Terres Australes et Antarctiques Françaises. The observations complied with the current laws of France. No eggs or chicks were abandoned during the course of this study.

RESULTS

Alert Distance (AD)

On average, focal individuals became alert when the experimenter came to a distance of 6.94 ± 0.18 m; (range = 1.89 – 13.14 m) (Fig. 17A and 17B). The interaction between approach x colony and time of day^2 did not have a significant effect influencing AD ($F_{2,111.0} = 0.22$, $P = 0.802$ and $F_{1,90.9} = 0.02$, $P = 0.896$, respectively), were sequentially removed from the model in that order (least significant term removed first). The final model with time of day, weather PC1, weather PC2, speed of approach prior to AD, approach order and colony, as fixed effects explained 13% (marginal R^2) of the total variation, and including individual as a random effect explained 22% (conditional R^2) of the total variation in AD (LMM, n=133 observations, N=47 individuals, $1.63 < \text{VIFs} < 3.68$, among-individual $\sigma^2 = 0.37$; residual $\sigma^2 = 3.63$). We found no evidence that AD was significantly affected by the time of day ($F_{1,92.2} = 2.00$, $P = 0.160$), speed of approach ($F_{1,120.0} = 1.25$, $P = 0.267$), weather PC2 ($F_{1,98.8} = 2.90$, $P = 0.092$), colony ($F_{1,84.0} = 0.00$, $P = 0.982$), or approach order ($F_{2,106.0} = 2.14$, $P = 0.123$) (Fig 18A). However, AD was significantly influenced by weather PC1 ($F_{1,102.1} = 7.29$, $P = 0.008$) with individuals showing lower AD during warm and sunny conditions (Fig. 18B).

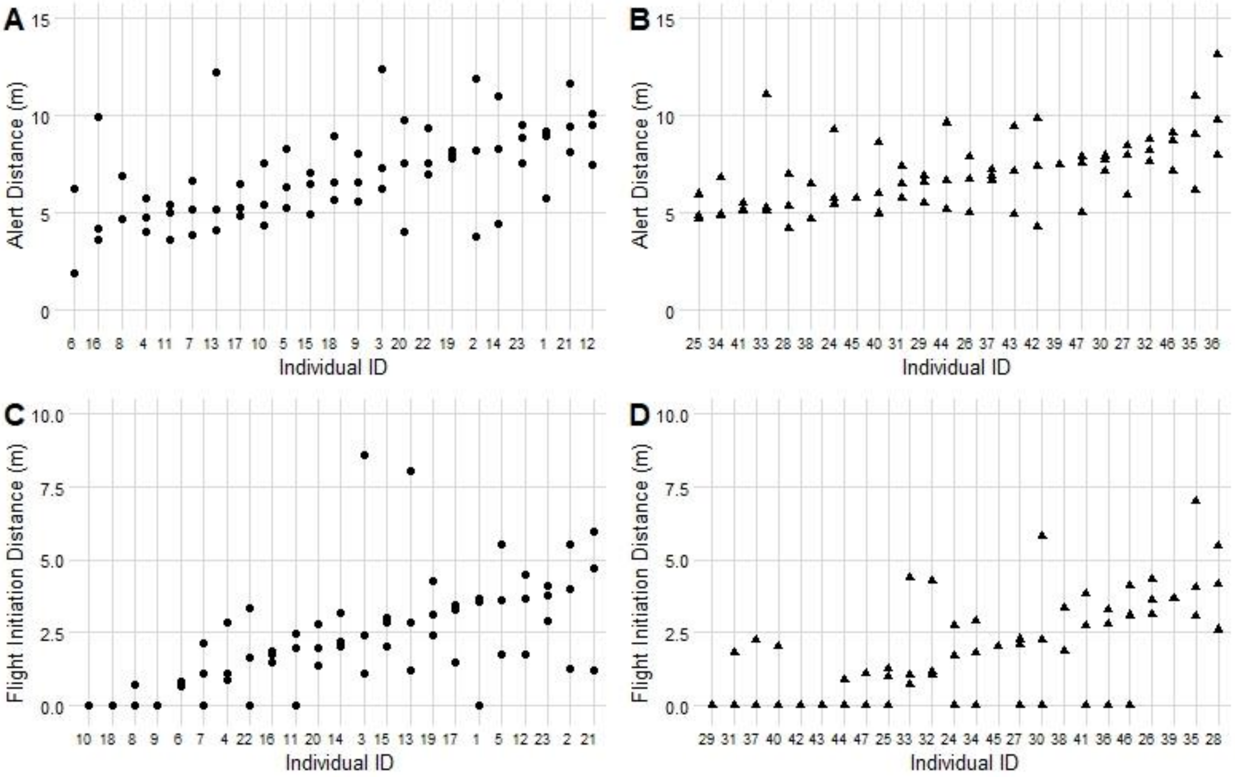

Figure 17. Scatter plots (generated from three observations per individual incubating king penguin, *Aptenodytes patagonicus*) of: A) Alert Distance (AD) in the Jardin Japonais colony (JJ; N = 23 individuals; circles); B) AD in the Baie du Marin colony (BDM; N = 24 individuals, triangles); C) Flight Initiation Distance (FID) in the JJ colony (N = 23 individuals); and D) FID in the BDM colony (N = 24 individuals), on Possession Island in the Crozet Archipelago. Individuals are ranked from lowest to highest mean scores of AD and FID per colony to allow for the visualisation of within versus among individual variability.

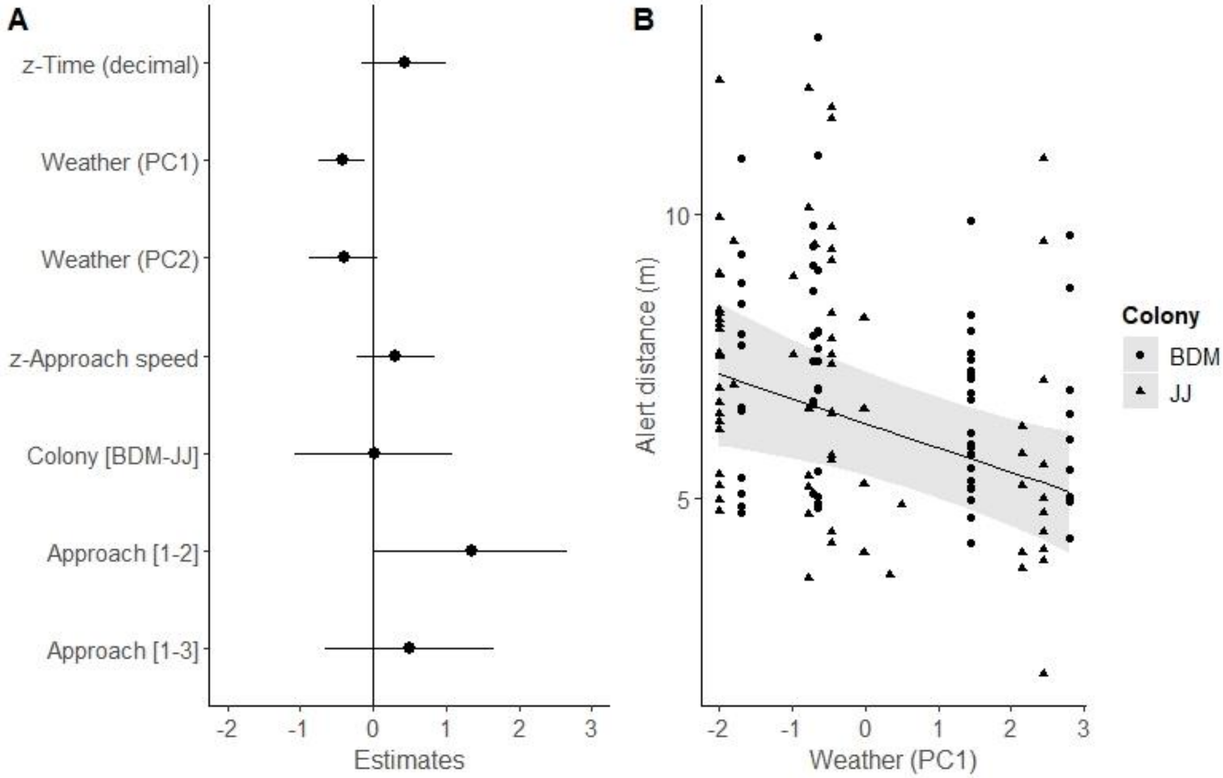

Figure 18. Variables affecting Alert Distance (AD) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of time of day (z-time), weather (PC1 and PC2), speed of approach prior to AD (z-speed), colony of origin (Baie du Marin, BDM, or Jardon Japonais, JJ), and approach number. n = 133 observations, N = 47 individuals. B) The significant predicted effect of weather PC1 on AD is depicted. Dots represent the raw AD values (BDM = circles, JJ = triangles); shading represents a 95% confidence interval predicted from the model while holding other variables in the model constant. A high weather PC1 value is associated with less rain, higher temperature, more sun, and more wind.

AD was not significantly repeatable when analysed on its own (r = 0.103; CI_{95} = [0, 0.290]; P = 0.146), but repeatability was close to significant after adjusting for weather (PC1) as a fixed effect (r_{adj} = 0.145; CI_{95} = [0, 0.313]; P = 0.062). Although some individuals appeared to be repeatable, many others displayed large variability in their AD (Fig. 17A and 17B). Post-hoc power analyses (see Appendix 1) revealed that significant repeatability (power 0.8) for AD may be achieved for a sample size of 6 approaches on 47 birds – or 3 approaches on 140 birds.

Flight Initiation

Out of the 47 selected individuals, 41 (87.2%) decided to flee (i.e., move away with their egg on their feet) during at least one of their approaches (20 birds in JJ, and 21 birds in BDM): 23 individuals always fled, 12 individuals fled twice in three approaches, 6 fled once in three approaches, and 6 did not flee at all. This corresponded to 42 approaches out of a total of 135 (31%) that resulted in no FID. The FID of the individuals that decided to flee at least once was 2.83 ± 0.16 m (range = 0.68 – 8.58 m) (Fig. 17C and 17D).

Time of day^2 and the interaction between approach x colony did not significantly influence the odds of fleeing (1) or not (0) during the approach (GLMMs; binomial, $\chi^2 = 2.35$, $P = 0.125$ and $\chi^2 = 4.97$, $P = 0.083$), and were sequentially removed from the model in that order (least significant term removed first). The final model with time of day, speed of approach between AD and FID, weather PC1 and weather PC2 explained 23% (marginal R^2) of the total variation, and including individual as a random effect explained 73% (conditional R^2) of the total variation in the odds of fleeing (GLMM, n=133 observations, N=47 individuals, 1.18 < VIFs < 5.36, among-individual $\sigma^2 = 3.29$; residual $\sigma^2 = 6.11$). The odds of fleeing were not significantly influenced by weather PC1 ($\chi^2 = 0.24$, $P = 0.626$), time of day ($\chi^2 = 1.19$, $P = 0.275$), speed of approach ($\chi^2 = 1.86$, $P = 0.172$), approach order ($\chi^2 = 4.98$, $P = 0.083$) or colony ($\chi^2 = 3.09$, $P = 0.079$). (Fig. 19A). However, the probability of birds to flee increased significantly with increasing weather PC2 ($\chi^2 = 4.51$, $P = 0.034$), birds being more likely to flee from the approaching experimenter in windy and rainy conditions (Fig. 19A and 19B). The decision to flee was significantly repeatable before (original-scale: $r = 0.504$; $CI_{95} = [0.084, 1.724]$; $P<0.001$) adjusting for weather, and increased slightly ($r = 0.573$; $CI_{95} = [0.110, 1.686]$; $P<0.001$) after accounting for the significant effect of weather PC2.

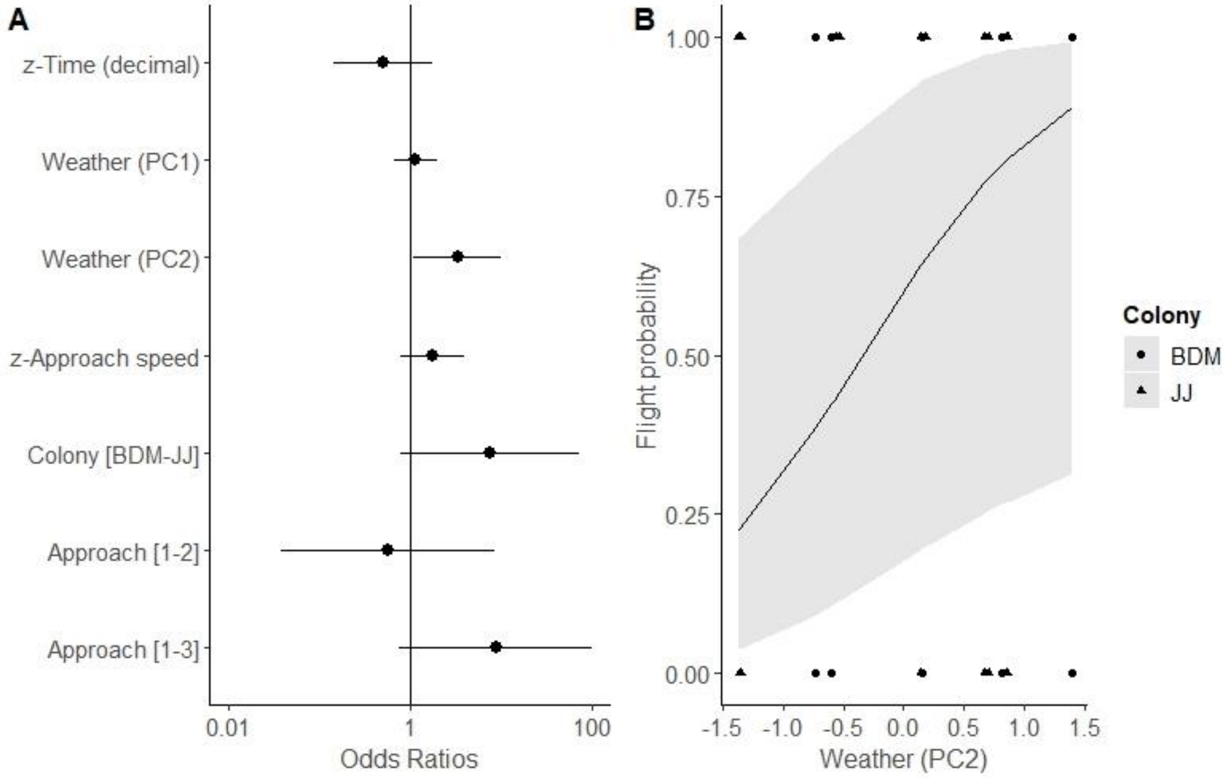

Figure 19. Variables affecting the decision to flee (binomial; 0 = no flight initiated, 1 = flight initiated) in incubating king penguins (*Aptenodytes patagonicus*). A) Odds ratios and 95% confidence intervals for time of day (z-time), weather (PC1 and PC2), speed of approach between AD and FID (z-speed), colony of origin (Baie du Marin, BDM, versus Jardin Japonais, JJ), and approach number. n = 133 observations, N = 47 individuals. The odds ratio can be interpreted for a given predictor in terms of increasing (>1) or decreasing (<1) the likelihood to flee for a one-unit increase in that predictor, holding all other variables constant. B) The significant predicted effect of weather PC2 on flight probability is depicted along with its 95% confidence interval (shading). Dots represent raw values separated by colony (BDM = circles, JJ = triangles). High weather PC2 is associated with increased rain and wind.

For those birds that decided to flee, time of day^2 and the interaction between approach x colony did not significantly influence FID during the approach (LMMs; $F_{1,66.5} = 0.15$, $P = 0.704$ and $F_{2,67.8} = 0.48$, $P = 0.619$, respectively), and were sequentially removed from the model in that order (least significant term removed first). The final model with time of day, speed of approach between AD and FID, weather PC1 and weather PC2 explained 37% (marginal R^2) of the total variation, and including individual as a random effect explained 62% (conditional R^2) of the total variation in FID (LMM, n=91 observations, N=41 individuals, 1.19 < VIFs < 5.56, among-individual σ^2 = 0.13; residual σ^2 = 0.09). We found no evidence that FID was significantly affected by the time of day ($F_{1,79.3}$ = 0.122, P = 0.727), weather PC1 ($F_{1,67.5}$ = 2.16, P = 0.146), colony ($F_{1,47.2}$ = 0.77, P = 0.384), or approach order ($F_{2,63.8}$ = 2.17, P = 0.123) (Fig 20A). However, FID increased significantly with the speed of the approach ($F_{1,71.8}$ = 31.64, P<0.001, Fig. 20A and 20B) and decreased significantly with increasing weather PC2 ($F_{1,60.6}$ = 5.17, P = 0.027, Fig. 20A and 20C). In other words, FID decreased in windy and rainy conditions. Agreement FID repeatability was low and not significant (r = 0.102; CI_{95} = [0.00, 0.339]; P = 0.248), but increased significantly when approach speed and weather PC2 were adjusted for in the model (r_{adj} = 0.258; CI_{95} = [0.010, 0.511]; P = 0.022).

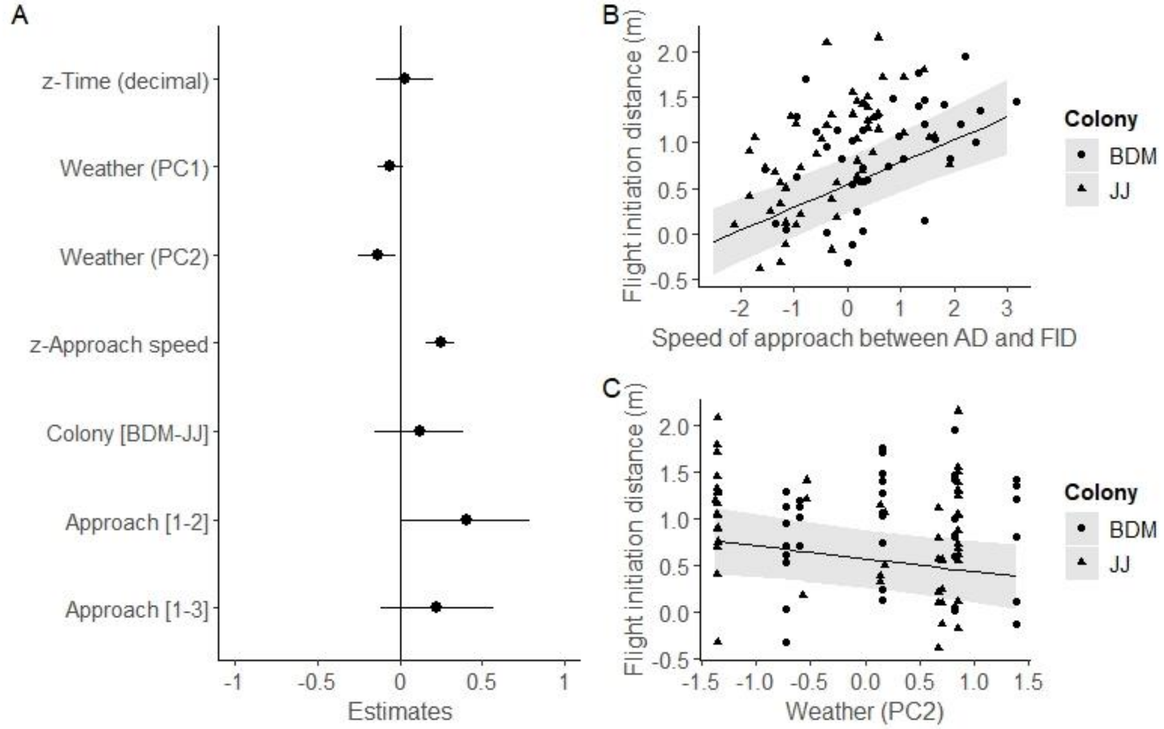

Figure 20. Variables affecting Flight Initiation Distance (FID) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervales (CI) for the effects of time of day (z-time), weather (PC1 and PC2), speed of approach between AD and FID (z-speed), colony of origin (Baie du Marin, BDM, or Jardin Japonais, JJ), and approach number. n = 91 observations, N = 41 individuals. B) The significant predicted effect of approach speed on FID is depicted along with its 95% CI. Dots represent raw FID values separated by colony, circles = BDM, triangles = JJ. C) The significant predicted effect of weather PC2 on FID is depicted along with its 95% CI. Dots represent raw FID values separated by colony, circles = BDM, triangles = JJ.

DISCUSSION

Our study showed that, in king penguins, both the decision to flee and FID were significantly and moderately repeatable, whereas AD was not. Climatic conditions had marked effects on AD, FID and the probability for birds to flee, affecting repeatability estimates, and highlighting the need to consider external sources of variation in refining such estimates in the wild (discussed below).

Between- and within-individual variation in flight initiation

Incubating king penguins showed significant (adjusted) repeatability both in the decision to flee from an approaching observer (0.57), and in the distance at which they initiated flight (0.26). In both cases, it is important to note that repeatability values increased when accounting for weather effects on behavior, which is not surprising since birds experienced different local climate conditions when they were approached. Notwithstanding, this underlines the importance of considering heterogeneity in individual habitats and timing of measures when establishing repeatability estimates from behavioral measures in the wild. Our repeatability values are comparable, albeit slightly lower, to those reported on FID in other studies: black swans*, Cygnus atratus* (r=0.61, van Dongen et al., 2015), juvenile yellow-bellied marmots, *Marmota flaviventris* (r=0.40, Petelle et al., 2013), Namibian rock agama, *Agama planiceps* (r=0.71, Carter et al., 2012), and burrowing owl, *Athene cunicularia* (r=0.88, Carrete and Tella, 2010), and generally moderate as would be expected for behavioral traits (Bell et al., 2009). The repeatability of both the decision to flee, and the distance at which flight was initiated, suggest that these behavioural traits could constitute good candidates for personality traits in breeding king penguins. This remains to be further explored however, since our power to detect behavioral plasticity in AD and FID occurring over longer periods was limited by the fact that birds in our study were only measured over a short period of time (3 consecutive days), and were not previously known individuals. Separating the repeatable and plastic aspects of alert and flight behavior to approaching predators in king penguins would benefit from further studies on individually monitored population where simple measures such as AD and FID are incorporated into monitoring schemes allowing to test for repeatability and plasticity over the lifetime of individuals (Dingemanse et al., 2010; Dingemanse & Wright, 2020). Logistically, this would require permanent marking of individuals in order to follow them through a longer period of time and through different contexts. In addition, FID (and AD, see below) are likely to vary according to factors such as individual age, sex, stress responsiveness, or body condition (e.g. Seltman et al., 2012; Kalb et al., 2019). Testing for such factors in future studies should allow refining repeatability estimates, with repeatability increasing as more residual variation is accounted.

Repeatability estimates of individual propensity to flee and FID increased as extrinsic factors were accounted for in the models. This is not surprising, but highlights contrasting climate effects acting both on the propensity to flee (1/0) and on the distance at which birds initiated flight. Interestingly, weather PC2 (wind and rain) had opposite effects on these behavioral traits. As conditions were windier and rainier, birds were more likely to flee, but those that fled had lower FID. This suggests that birds that fled waited until the last moment before they did so, which could be explained by the fact that they were less likely to detect the incoming threat in windy and rainy conditions. Wind speed has been shown to have contrasting effects on animal vigilance and escape behavior, from no effect to marked effects depending on the species and taxa (e.g., no effect: birds; Clucas and Marzluff, 2011, Nordell et al., 2017, Petrelli et al., 2017; reptiles; McGowan et al., 2014; wind effects: birds; Reynolds et al., 2020; mammals; Wolf & Croft, 2010). Increased wind speed has been shown in 17 of 18 studies to decrease an animal's ability to detect an approaching predator by masking sounds, smells and visual cues (Cherry and Barton, 2017). Wind may also be a source of distraction (Chan et al., 2010; Tätte et al., 2019), leading to delayed detection of approaching predators. It has been suggested that the magnitude of FID responses should decrease under harsh weather conditions, as the energy cost of fleeing increases (Collop et al., 2016). For endotherms wind chill increases thermoregulatory costs, and a trade-off might exist between investing energy into flight and that into thermoregulation (Collop et al., 2016, but see also Reynolds et al., 2020).

Because penguins rely essentially on fat stores during incubation on-land (Groscolas & Robin, 2001), and because energy-depleted birds will abandon reproduction (Groscolas et al., 2000, Gauthier-Clerc et al., 2001), any energy savings – however small – is critical. Thus, energy savings in harsh climate conditions may contribute in explaining why birds waited for the last moment to flee. FID also increased with increasing approach speed of the experimenter. Faster approach speeds after alert may be interpreted as greater threat by the targeted prey, and thus generating longer FID (Stankowich and Blumstein, 2005; Cooper and Whiting, 2007; Smith-Castro and Rodewald, 2010; Bateman and Fleming, 2011).

It is interesting to note that it was not uncommon for the incubating penguins to stay and defend their eggs aggressively instead of attempting to flee (there was an FID of 0 m in 42 approaches of 135). For these birds either the perceived risk of the approaching threat (a human) was not high enough to elicit a flight response, or the motivation to breed and defend the territory was stronger than that of attempting to flee. FIDs of 0 m have been observed in other ground laying birds: yellow-eyed penguins *Megadyptes antipodes* (Ellenberg et al., 2007, 2009), Humboldt penguin *Spheniscus humboldti* (Ellenberg et al., 2006), Magellanic penguins *Spheniscus magellanicus* (Fowler, 1999; Villanueva et al., 2014), and African penguins *Spheniscus demersus* (Pichegru et al., 2016). King penguins are special in that they incubate their egg on their feet in a specialized brood pouch. Thus, fleeing is at any rate limited, and essentially amounts to clustering close to neighbours in the hope to benefit from confusion, dilution or selfish herd effects. In addition, fleeing may risk damaging or losing the egg, losing the breeding territory, suffering from increased aggression by territorial neighbours (Côté, 2000), or disturbing the thermal incubation environment required for chick development and survival. For instance, exposed eggs during transitory breeding abandonment in king penguins have been found to lose heat at a rate of 0.19 °C per minute (Groscolas et al., 2000).

Between- and within-individual variation in AD

In contrast to FID, the repeatability of AD was low (0.10) and not significant, but improved slightly (0.15) and was close to significant (*P* = 0.062) when accounting for the effects of climate (Weather PC1). As far as we are aware, there is no report of the repeatability of AD in the literature. Rather, researchers have considered vigilance behaviour when aiming to understand how animals respond to threats. More vigilant individuals are expected to detect predators earlier and thus become alert at longer distances (Fernández-Juricic and Schroeder, 2003; Beauchamp, 2015; Uchida et al. 2019; but see Tätte et al., 2019). Studies that measured repeatability in vigilance behaviours also reported low, but significant, repeatability: eastern grey kangaroos, *Macropus giganteus*, (*r*=0.07-0.14, Edwards et al., 2013); redshanks, *Tringa totanus*, (*r*=0.21, Couchoux and Cresswell, 2012); house sparrows, *Passer domesticus*, (*r*=0.13-0.22, Boujja-Miljour et al., 2018); cliff swallows, *Petrocheldion pyrrhonota*, (*r*=0.089, Roche and Brown, 2013). As mentioned above, repeatability estimates are likely to increase as some residual variation is accounted for by including potential factors such as age, sex, or condition, that were unfortunately not available in this study as individuals were not followed or handled. Dingemanse and Dochtermannn (2013) determined that for lower repeatabilities, >4 samples per individual were required if the total number of individuals is <100. Similarly, Wolak et al. (2012) found fewer samples per individual were required for higher r values (3 samples per individual for an *r* of 0.8), but for an *r* of 0.2, the precision of the estimate continues to increase until up to 10 samples per individual. Because of time and field constraints we were only able to repeatedly approach 45 individuals 3 times. Yet, post-hoc power analyses revealed that doubling our sample size to 6 repeated measures per bird would have been sufficient to detect significant repeatability. At any rate, repeatability was low, indicating that individuals were more flexible in this behavioral trait than in their decision to flee. Similarly, vigilance levels (and presumably AD) have been found to be highly flexible (Couchoux and Cresswell, 2012; Edwards et al., 2013) and sensitive to numerous biological factors such as group position and group size, distance to cover, predation pressure, season, weather, and time of day (reviewed in Elgar, 1989). In our study, AD was significantly lower in warm and sunny conditions, suggesting that birds were less vigilant in good weather conditions.

Colony disturbance, predation pressure and STRANGE animals

We expected AD and FID to vary depending on colony and with changes in predation pressure throughout the day. However, our analyses suggests that neither were major factors influencing escape decisions in the king penguin. First, on-land predation in king penguin colonies is highest at dawn and dusk (Le Bohec et al., 2003; Descamps et al., 2005), whereas most of our measures were done between 8 AM and 6 PM. Extending measurements to early morning and late evening when predators are most active may allow to better capture potential effects of predation pressure on penguin behavior. Second, given that the two colonies surveyed in this study differ markedly in their exposure to human presence throughout the year (BDM is located next to a research station and breeders have seen humans almost every day for the past 50 years, whereas birds in JJ are rarely exposed to human visitors), we had expected birds in the BDM (vs. JJ) colony to habituate to approaching humans. However, the lack of difference in behavioral responses between the colonies is perhaps not so surprising. Previous findings indicate that birds breeding in more disturbed areas of the BDM colony show lower heart rate stress responses to an experimenter approaching to 10 m distance than birds in less disturbed areas – suggesting a potential for habituation to the presence of humans in chronically disturbed areas (Viblanc et al., 2012). Yet, heart rate responses were similar between the disturbed and undisturbed areas when birds were approached up to contact and captured (Viblanc et al., 2012). Although birds were not captured in the present study, they were approached up close (to a few cm), and the risk assessed was presumably more comparable to a capture than to an observer standing some 10 m distant.

Previous studies in similar seabirds have shown contrasted responses to human approaches. For instance, whereas Magellanic (*Spheniscus magellanicus*), African (*S. demersus*), and Gentoo penguins

(*Pygoscelis papua)* show reduced behavioural and/or physiological responses (heart rate or corticosterone concentrations) to human visitation in high disturbance areas (van Heezik and Seddon, 1990; Fowler, 1999; Walker et al., 2005, 2006; Holmes et al., 2006; Villanueva et al., 2012; Pichegru et al., 2016), yellow-eyed penguins (*Megadyptes antipodes*) appear to sensitize to human exposure through higher stress responses (Ellenberg et al., 2007). Taken together, these results highlight two important points: (1) behavioural and physiological responses to approaching predators (or humans) may tell seemingly different stories. A proper understanding of prey responses to approaching predators requires the integrative assessment of both physiological stress responses and behavioural reactions. (2) both behavioural and physiological responses are fine-tuned mechanisms integrating risk assessment into optimal escape decisions.

Finally, we must consider how STRANGE were the animals in our study (Webster & Rutz 2020). We selected birds in the colonies haphazardly, with no knowledge of their sex, age or past experience. Nonetheless we did not capture and measure bird morphometrics in our study, but visually targeted birds that appeared in overall good physical condition in order to minimize the risk of breeding abandonment for energy-depleted birds (Groscolas et al., 2000, Gauthier-Clerc et al., 2001) in this protected species. Our measures on individual birds were done over a few days during which changes in body condition were likely relatively minor. However, we might not have captured the full range of behavioral expression of AD and FID, particularly for birds of low body condition. This is important to consider since individuals in poor body condition may have enhanced stress and FID responses to approaching experimenters (Seltmann et al., 2012), and emphasizes the importance of controlling for body condition – where feasible – in performing repeated measures on wild animals.

As this study only tested the response to repeated approaches in two colonies, which will have obvious differences in colony size, density, and topography, replicating this study over additional colonies would help in a better characterisation of the factors shaping escape decisions in penguins. In addition to landscape and social differences between colonies, there are also possible differences in predation pressure and genetic differentiation. Furthermore, the sampling in the two colonies took place 20 days apart, allowing for possible differences in the reproductive cycle to manifest. Lastly, sampling only occurred over a span of three days. Further studies should investigate these factors in more depth, as well as test repeated approaches over a longer time period – and over the lifetime of individual birds. In particular, these would help in capturing a greater range of weather conditions, and better understanding the extent of repeatability and plasticity of these behavioral traits (Dingemanse & Wright, 2020).

The response of a wild population to human disturbance creates special considerations in a world that is increasingly accessible to humans. Ecotourism and wildlife tourism, or travel to natural areas to engage in shared experiences with wildlife and whose aim is to conserve the environment through education and local spending, are increasingly common activities. As a charismatic anthropomorphic animal, penguins have garnered much attention. In many species, habituation occurs in response to disturbances caused by tourists (van Heezik and Seddon, 1990; Fowler, 1999, Holmes et al., 2006; Villanueva et al., 2014). However, even in species that have habituated to disturbance, human presence can impact natural behaviours, time budgets, heart rates and stress levels (Holmes et al., 2005; Walker et al., 2005, 2006; Burger and Gochfeld, 2007; Viblanc et al. 2012; Villanueva et al., 2012; Pichegru et al., 2016). For species that cannot habituate or which have sensitized to disturbance, individuals may experience negative impacts on their reproductive success ultimately endangering the population as a whole (Giese, 1996; McClung et al., 2004; Ellenberg et al., 2006, 2007, 2012, 2013; Carroll et al., 2016). Knowledge of AD and FID may help inform policy makers when deciding appropriate viewing guidelines for tourists (Ellenberg et al., 2006, French et al., 2019).

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Chapter 2

Disentangling the “many-eyes”, “dilution effect”, “selfish herd”, and “distracted prey” hypotheses in shaping alert and flight initiation distance in a colonial seabird

Tracey L Hammer[1], Pierre Bize[2], Benoit Gineste[1,3], Jean-Patrice Robin[1], René Groscolas[1], Vincent A Viblanc[1]

[1]University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000 Strasbourg, France

[2] Director of Research, Vogelwarte, Sempach, Switzerland

[3]IPEV – Institut Polaire Français Paul Émile Victor, 29280 Plouzané, France

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ABSTRACT

Group living is thought to have important antipredator benefits for animals, owing to the mechanisms of shared vigilance (“many-eyes” hypothesis), risk dilution (“dilution effect” hypothesis), and relative safety in the center of the group (“selfish herd” hypothesis). However, it can also incur costs since social stimuli, such as conspecific aggression, may distract individuals from anti-predator behavior (“distracted prey” hypothesis). We simultaneously tested how these four different hypotheses shape anti-predator behaviors of breeding king penguins (*Aptenodytes patagonicus*), which aggregate into large colonies, experience frequent aggressive social interactions, and are regularly exposed to predators. We experimentally approached 200 incubating penguins at four different periods of the breeding season across a range of overall increasing colony densities. We measured the distance at which focal birds detected the approaching threat (alert distance: AD), whether birds decided to flee or not, and the distance of flight initiation (flight initiation distance: FID). We quantified relative local neighbor density, centrality within the colony (rank), and the number of aggressions the focal bird emitted towards neighbors during the approach. We found that birds engaged in aggressive conflicts with neighbors were less likely to flee, and that increasing relative local neighbor density at low and medium overall colony density resulted in a decrease in bird AD, both supporting the “distracted prey” hypothesis. However, at maximal overall colony density, increasing relative local neighbor density resulted in longer AD, supporting the “many-eyes” hypothesis. We found no support for the “dilution effect” and “selfish herd” hypotheses, and no effects of any hypothesis on FID.

Key words: antipredator behaviour, escape flight distance, optimal escape decisions, predation risk, predator-prey decision, risk taking

INTRODUCTION

Predation can be an important source of mortality in wild animals (Roos et al. 2018). Aggregating into large social groups is often viewed as a solution used by animals to decrease predation risk for the individual and its offspring (Alexander 1974; Hoogland 1981). At least four non-mutually exclusive hypotheses have been proposed to explain how group size and social interactions may influence predator-prey interactions (for a review of the relationship between group size and flight initiation distance, see Ydenberg and Dill 1986; Stankowich and Blumstein 2005).

Firstly, one important mechanism identified in decreasing predation risk with increasing group size is that of shared vigilance by group members towards potential threats (Caraco et al. 1980; Lima and Dill 1990; Quenette 1990). Since larger groups have more individuals scanning for predators at any given time, the presence of "many eyes" in a group allows for the earlier detection of predators than would be possible for single individuals (the "many-eyes hypothesis"; Pulliam 1973; Lima and Dill 1990). Information on the presence of a predator can disseminate rapidly through the group, most often through the use of alarm calls, allowing individuals to assess the risk and decide to flee sooner than is possible alone (Burger and Gochfeld 1991; Mayer et al. 2019). Thus, larger groups are often more rapid in detecting a predator than single individuals, and are more likely to raise alarm of an approaching predator sooner than smaller groups (Hoogland 1981; van Heezik and Seddon 1990; Cresswell 1994).

Secondly, large groups also provide the advantage of diluting individual predation risk (Ydenberg and Dill 1986). Most predatory species can only capture a single prey at a time, and thus the chance that each individual prey will be the target of predation reduces with increasing group size (Dehn 1990; Roberts 1996; Bednekoff and Lima 1998). According to the "dilution effect hypothesis" individuals in larger groups may tolerate the closer approach of predators before initiating flight (enabling a longer amount of time to be spent on tasks such as foraging), since the risk of predation is diluted with each additional conspecific nearby (Cresswell 1994; Boland 2003; Fernández-Juricic and Schroeder 2003). The dilution effect is not only limited to larger group sizes, but also, of course, to denser groupings of individual prey, regardless of overall group size (Roberts 1996; Hebblewhite and Pletscher 2002; Frommen et al. 2009). For example, many bird species that migrate in flocks or cluster together on breeding grounds may benefit from the dilution effect by reducing individual predation risk while foraging or breeding (Wiklund and Andersson 1994; Harts et al. 2016; Duca et al. 2019).

Thirdly, individual spatial positioning within the group may provide dissimilar anti-predator benefits. The "selfish herd" hypothesis (Hamilton 1971) suggests that animals located more centrally in a group should be less vulnerable to attacks from predators than those on the periphery as predators come from outside the group and target the closest available prey (Hamilton 1971). In other words, maintaining conspecifics between a predator and oneself will reduce individual predation risk. Prey animals should therefore select higher value central positions when joining a group, which is indeed seen in minnows, *Phoxinus phoxinus* (Krause 1993), sheep, *Ovis aries* (King et al. 2012), and fiddler crabs, *Uca pugilator* (Viscido and Wethey 2002). If selfish herd effects are important, there should be evidence of divergent predation rate, pressure or risk between the center and the periphery of a group (Morton et al. 1994; Viscido et al. 2001). When redshanks, *Tringa tetanus*, were targeted by sparrowhawks, *Accipiter nisus*, birds that were more peripheral and further from neighbors were at the highest risk of predation (Quinn and Cresswell 2006). In colonial web-building spiders, *Meteperira incrassata*, predatory attacks occur most often on the periphery (Rayor and Uetz 1990). There may also be evidence of different levels of investment by prey into anti-predator monitoring between central and peripheral animals. Increased vigilance by peripheral animals has been observed in black-tail prairie dogs, *Cynomys ludovicianus* (Hoogland 1981), African mammals (Burger and Gochfeld 1994), including springbok, *Antidorcas marsupialis*, (Bednekoff and Ritter 1994), and scaled doves, *Columbina squammata* (Dias 2006).

Finally, although larger groups provide the benefit of shared vigilance and predation risk dilution, individuals in such groups have to process a noteworthy amount of social information from their conspecifics (Treves 2000). As a consequence, the time spent processing social cues and interacting with conspecifics, noise and conflicts from and between conspecifics may detract from the time and energy investments usually placed into scanning for predators (Mooring and Hart 1995; Yee et al. 2013). This is known as the “distracted prey hypothesis” which proposes that external stimuli are capable of hijacking finite resources, thus impairing the prey’s ability to detect and react to approaching predators (Chan et al. 2010; Petrelli et al. 2017). Social distractions (such as aggressive interactions between conspecifics) may distract prey from predator detection and delay behavioral responses such as the initiation of flight. This is, for instance, the case in a cichlid fish species (*Neolamprologus pulcher*), where individuals respond significantly later to predator images during territorial contests than when they are alone, illustrating the trade-off between time and energy investments into aggressive social behaviors and vigilance towards predators (Hess et al. 2016).

In this study, we investigated simultaneously the relative importance of the “many-eyes”, “dilution effect”, “selfish herd” and “distracted prey” hypotheses on prey anti-predator behaviors of breeding king penguins (*Aptenodytes patagonicus*). King penguins are an ideal model system to test these non-mutually exclusive alternatives. This seabird species forms extensive, densely packed colonies when breeding on land (over tens of thousands of birds strong, Barbraud et al. 2020). Breeding birds incubate/raise a single egg/chick on their feet and aggressively defend their small breeding territory against both predators and conspecifics (Stonehouse 1960; Weimerskirch et al. 1992). Aggressive social interactions are particularly high and can average 100 interactions per hour (Côté 2000). Of particular interest is the finding that king penguins are highly sensitive to social aggression, even when they are not directly involved in social conflicts (as demonstrated by elevated by-stander heart rate responses when witnessing aggressive neighbors fighting (Viblanc et al. 2012). In addition, higher stress hormones and heart rates are detected in more densely packed colony areas (Viblanc, Gineste, et al. 2014; Viblanc, Saraux, et al. 2014). Thus, frequent social aggression in these birds may interfere with antipredator behaviors, such as vigilance and flight. King penguins are subject to on-land predation by giant petrels, *Macronectes giganteus* and *Macronectes halli*, and brown skuas, *Catharacta loonbergi*, especially known to predate on eggs and young chicks, but occasionally targeting adults as well (Hunter 1991; Descamps et al. 2005). Yet, how acute social interactions ("distracted prey" hypothesis), safety in large numbers ("dilution effect" hypothesis), safety in a central location ("selfish herd") and shared vigilance ("many-eyes" hypothesis) interact in shaping prey antipredator behavioral responses is unknown.

Here we used Alert Distance (AD), or the distance at which the targeted bird detects an approaching threat (in this case, an experimenter), and Flight Initiation Distance (FID), or the distance at which the targeted bird begins to flee from the approaching threat to simultaneously investigate the "many-eyes", "dilution effect", "selfish herd" and "distracted prey" hypotheses. AD and FID are popular measures used in the literature to study the reactions of prey to approaching danger and optimal escape strategies. The great advantage of these measures is that they can be collected through non-lethal approaches by a human experimenter using standardized approach protocols (see Hammer et al. 2022 for an example of this approach method, which also happens to be the first study of AD and FID in king penguins). From an evolutionary perspective, prey are expected to react in much the same way to a human approach as to an approach by a true predator, as behavioral responses should be selected to over-estimate rather than under-estimate risk (Frid and Dill 2002; Beale and Monaghan 2004). AD and FID are therefore promising behavioral responses that can be used to better understand how group size and social interactions may shape predator-prey interactions.

We evaluated AD and FID in response to standardized human approaches in relation to both overall colony density (low, med, high, maximal) that increased as the breeding season progressed, relative local neighbor density (number of neighbors around a focal bird centered around the mean overall colony density at any given stage of the season), relative colony rank (rank centered with each colony density stage), and the number of aggressive interactions (i.e., social distractions) exchanged between the focal bird and its neighboring conspecifics during the approach. Whereas the “many eyes” hypothesis predicts that AD should occur earlier in larger or denser groupings as there are more vigilant individuals present at any given point in time, the “distracted prey” hypothesis predicts that AD and/or FID will be delayed in denser groups due to increased social stimuli, such as aggression with neighbors, that hinders predator detection and flight. The “selfish herd” hypothesis predicts that peripheral individuals in the colony (those of low colony rank as counted from the periphery to the center of the colony) where predation risk is highest, will have higher AD and FID than individuals in less risky central positions. Finally, the “dilution effect” predicts that FID will be delayed at high local social density due to reduced predation risk on the individual, but should be unrelated to social interactions (social aggression, in our case). Predators may be allowed to approach even closer in aggressive groupings of prey than the dilution effect predicts alone, as is the case in king penguins, as larger groups may allow for group defense from predators (i.e., mobbing).

METHODS

Study site and animals

During the 2011-2012 breeding season, 200 king penguins were randomly approached in “La Baie du Marin” colony (Possession Island, Crozet Archipelago, 46°25’S – 51°52’E), home to approximately 22 000 breeding pairs (Barbraud et al. 2020). According to STRANGE guidelines (Webster and Rutz 2020), study subjects were selected to reduce potential biases (and were hence not blindly selected), nevertheless we highlight some of the potential biases here. All birds were incubating and therefore of similar breeding status (but see discussion) and appeared in physically good overall condition; but we did not have any information on bird age, sex, laying date, or previous exposure to humans. Individuals were chosen from a distance and not after being approached or captured, therefore we expect no strong initial sampling bias. The individuals were divided into four groups of 50 birds, measured approximately 15 days apart from mid-November 2011 to mid-January 2012. As colony density increases over the breeding season (see Viblanc et al. 2014b for colony dynamics), our objective was to sample birds in natural conditions of increasing social density. Thus, we defined four groups corresponding to periods of increasing overall colony density with: low density (mean ± SE birds/m^2: 4.05 ± 0.11, 19-22 Nov. 2011), medium density (4.48 ± 0.14, 3-5 Dec. 2011), high density (5.04 ± 0.11, 22-23 Dec 2011), and maximal density (5.47 ± 0.11, 13-16 Jan 2012).

Approach protocol

Approaches (always the same experimenter, BG, dressed in the same clothing) were started at a standardized start distance of 18 m when the focal individual was awake. A distance of 18 m corresponded to a distance 1.5 times greater than maximal detection distance recorded in a preliminary study to ensure starting distance far exceeded maximum alert distance (Hammer et al. 2022, see also Fleming and Bateman 2017). Start distance was standardized due to its known effect on AD and FID (Blumstein 2003; Blumstein 2010; Dumont et al. 2012). Distances were measured to the nearest cm using a laser telemeter (Leica DISTO^{TM} D5 Lasermeter, Leica Geosystems AG, Hexagon, Sweden). The experimenter, while walking at a regular speed, followed a direct trajectory towards the focal individual. Both when the first sign of detection was observed (AD; focal animal tilting its head or stretching its neck in the direction of the experimenter), and when flight was initiated (FID; focal animal attempting to walk away with its egg on its feet), the experimenter took a standardized one-minute pause to record the distance between his position and the bird. Several focal birds did not flee up until contact. Thus, FID was divided into two separate analyses: *i*) the decision to flee or not, and *ii*) the flight initiation distance for birds that decided to flee. During the approach, the number of aggressive interactions initiated by the focal bird towards its neighbors was recorded as a proxy of social distraction. This value was then weighted by energy expenditure such that physical aggressions weighed more heavily than non-physical threats; according to Viera et al. (2011), contact aggressions are 3.2 times more energy consumptive than threat aggressions (mean ± SE = 0.69 ± 1.00, range = 0.0 – 5.2).

Two speeds of approach (prior to AD and prior to FID) were calculated using the distance walked (m) and the duration of approach (s). The mean ± SE speed of approach prior to AD was 0.51 ± 0.07 m/s (range = 0.28 – 0.76 m/s), and between AD and FID was 0.42 ± 0.05 m/s (range = 0.24 – 0.54 m/s). Weather conditions were recorded prior to each approach and used as control variables in the analyses (Hammer et al. 2022). Air temperature was recorded to the nearest 1°C, and wind and rain levels were scored between 0 (none) and 2 (strong or heavy), intermediate levels (0.5) being allowed.

Before approaching the birds, we counted the number of neighbors surrounding each focal individual, defined as the first circle of animals that were direct neighbors (mean ± SE = 7.49 ± 1.93; range = 4 - 14) and recorded the mean distance of the neighbors to the focal individual (mean ± SE = 0.81 ± 0.14; range = 0.53 – 1.22 m). The distance between the birds was initially visually estimated from a distance and subsequently corrected to the closest 10 cm during the approach. Local density (number of birds/m^2) was then calculated as the number of neighbors surrounding a focal bird divided by the area of a circle (πr2) with the mean distance between the focal bird and its neighbors acting as the radius. Local bird density increased with overall colony density ($F_{3,192}$=28.0, P<0.001) (Fig. 21). As local neighbor density naturally increased together with increasing colony density (i.e., low, medium, high, maximal) as the breeding season advanced, we centered local neighbor density within each colony density stage to obtain an index of local neighbor density which was independent of overall colony density. Thus, relative local neighbor density was calculated as d - $\mu\bar{d}$, with d being the local neighbor density of a focal bird, and $\mu\bar{d}$ being the mean neighbor density over all birds measured at a given stage (i.e., within low, medium, high, and maximal colony density stages). A bird with relative local neighbor density >0 (or <0) thus experienced a “local” social environment that was relatively more or less crowded than the average at a given stage.

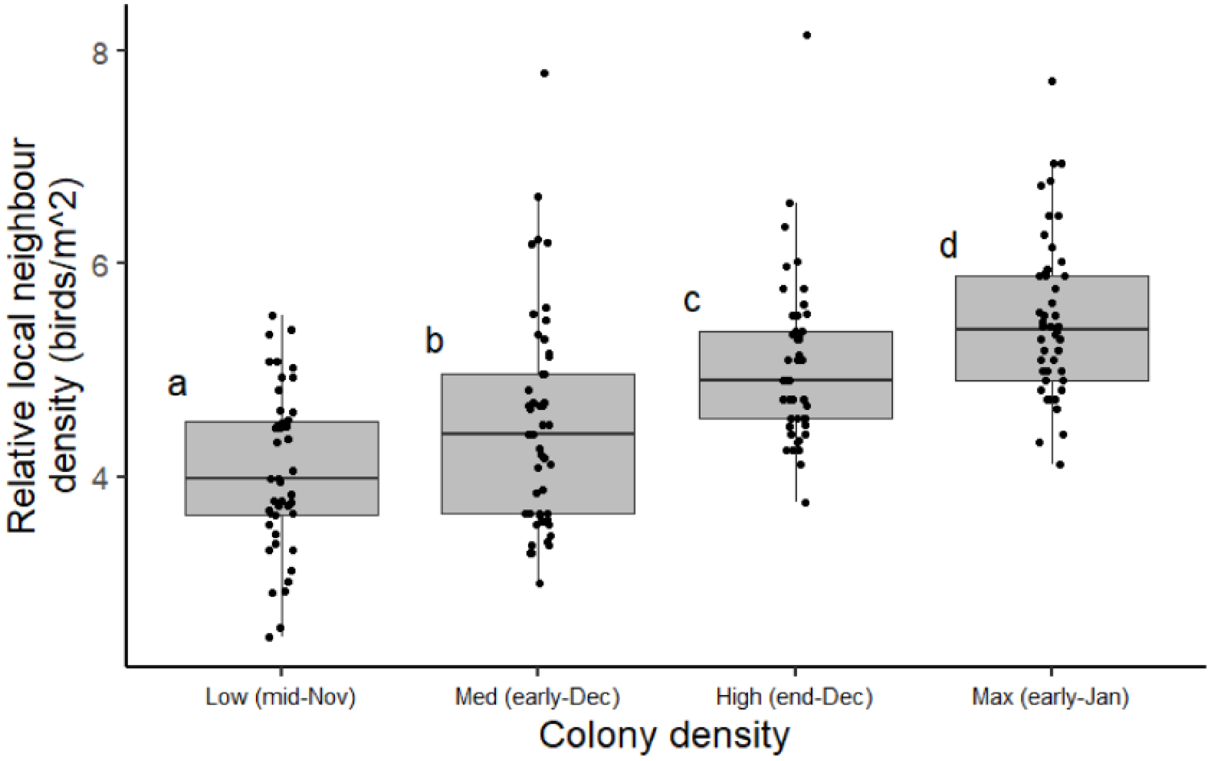

Figure 21. The linear relationship of colony density and relative local neighbour density in incubating king penguins (*Aptenodytes patagonicus*). Significant differences are distinguished using the letters a, b, c, d. Dots represent the relative local density values; the horizontal bar represents the median, shading represents the interquartile range, and the vertical line represents the 95% confidence interval.

Statistical analyses

All statistical analyses were performed in R 1.4.1106 (R Development Core Team 2021). Results are presented as means ± SE. We tested for the “many eyes”, the “dilution effect”, “selfish herd”, and the “distracted prey” hypotheses by considering the joint effects of overall colony density, relative local neighbor density, relative colony rank (see below), and number of aggressive interactions of the focal individual to their neighbor (all independent variables) on focal bird AD, FID, and decision to flee or not (all dependent variables in separate models). The number of aggressions displayed against neighboring individuals during the entire approach was used to quantify the amount of social distraction to which the focal birds were subject. Similar to relative local neighbor density, we calculated relative colony rank (or the relative centrality of the focal bird within the colony) by centering bird rank within each overall colony density stage (low, medium, high, maximal) in the manner of $r - \mu\bar{r}$, with r being the rank of a focal bird, and $\mu\bar{r}$ being the mean rank over all measured birds at a given stage. Thus, a bird with a relative colony rank >0 (or <0) was relatively more (or less) central in the colony than the average at a given stage. General linear mixed models with appropriate error distributions were used to investigate sources of variation in AD (gaussian distribution), the decision to flee or not (binomial distribution), and FID (gaussian distribution after log transformation). Models were run using the package “lme4” functions *lmer* and *glmer* (Bates et al. 2015). Models were checked for the normality of their residuals using “fitdistrplus” (Delignette-Muller and Dutang 2015). For models with a gaussian distribution, the significance of fixed effects were tested with “lmerTest” *anova* (Kuznetsova et al. 2017) using F tests with Satterthwaite estimation for the denominator degree of freedom. Wald chi-square tests were used for models with a binomial distribution (*Anova*). We further tested if behavioral decisions (AD, FID, and the decision to flee or not) were affected by the interaction between relative local neighbor density and overall colony density (low, medium, high, maximal); this interaction was dropped from the models if it was non-significant. The area of the colony in which we approached the bird was initially included as a random factor in all our models to control for unmeasured differences in landscape, chronic and spatially variable amounts of human disturbance, etc., and the fact that several birds were measured in similar areas. However, this random effect was removed from the binomial model as no variation in the decision to flee could be attributed, and the model could not converge. In all models we initially controlled for time of day (linear and quadratic effects, decimal), weather (temperature, wind and rain levels), and speed of approach to account for tentative effects on AD, FID, and the decision to flee

(Hammer et al. 2022), but removed them from the final models if they were non-significant. All independent variables were tested for collinearity using Variance Inflation Factors (VIF) according to the suggestions by Zuur et al. (2010) and all variables were scaled and centered prior to inclusion (Schielzeth 2010). Temperature was, in any case, removed from all the models due to collinearity issues with colony density as temperature generally increased as the summer season progressed and the breeding season advanced.

Ethics statement

No animal was caught or handled over the course of this study. The research was approved by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor. Authorization to enter the colony and approach birds was obtained from Terres Australes et Antarctiques Françaises. The observations complied with the current laws of France. No eggs or chicks were abandoned during the course of this study.

RESULTS

Over the entire season, individuals (N = 194) became alert on average ± SE at 7.31 ± 1.91 m; (range = 3.41 – 12.3 m). The interaction between relative local neighbor density and overall colony density was significant (LMM, $F_{3,173.3} = 2.84$, $P = 0.039$) (Fig. 22). AD decreased with increasing relative local neighbor density at low (slope and 95% confidence interval= -0.48 [-1.02, 0.06]) (Fig. 23). However, at medium (-0.46 [-95, 0.04]) and high (-0.12 [-0.71, 0.47]) overall colony density, there was no relationship between AD and relative local neighbor density. Finally, at maximal colony density AD increased with increasing relative local neighbor density (0.64 [0.02, 1.26]). AD was not significantly affected by the number of aggressive interactions between the focal individual and their neighbors ($F_{1,172.7} = 0.01$, $P = 0.905$), nor relative colony rank ($F_{1,175.0} = 0.00$, $P = 0.978$).

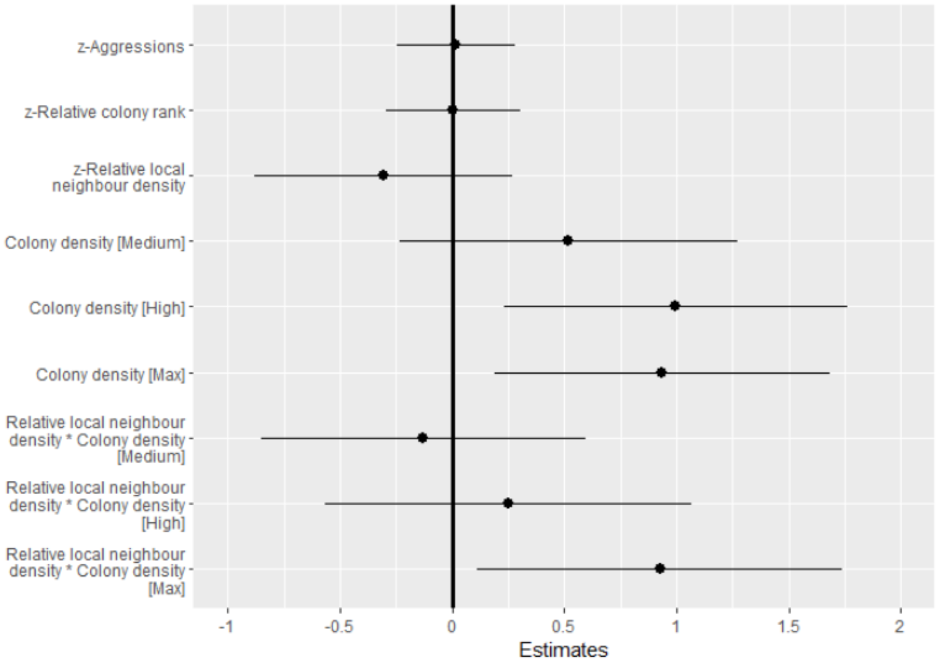

Figure 22. Variables affecting Alert Distance (AD) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of the number of aggressions with conspecifics, relative local neighbour density, colony density (low, medium, high, and maximal), and the interaction between relative local neighbour density and colony density (n = 194 observations).

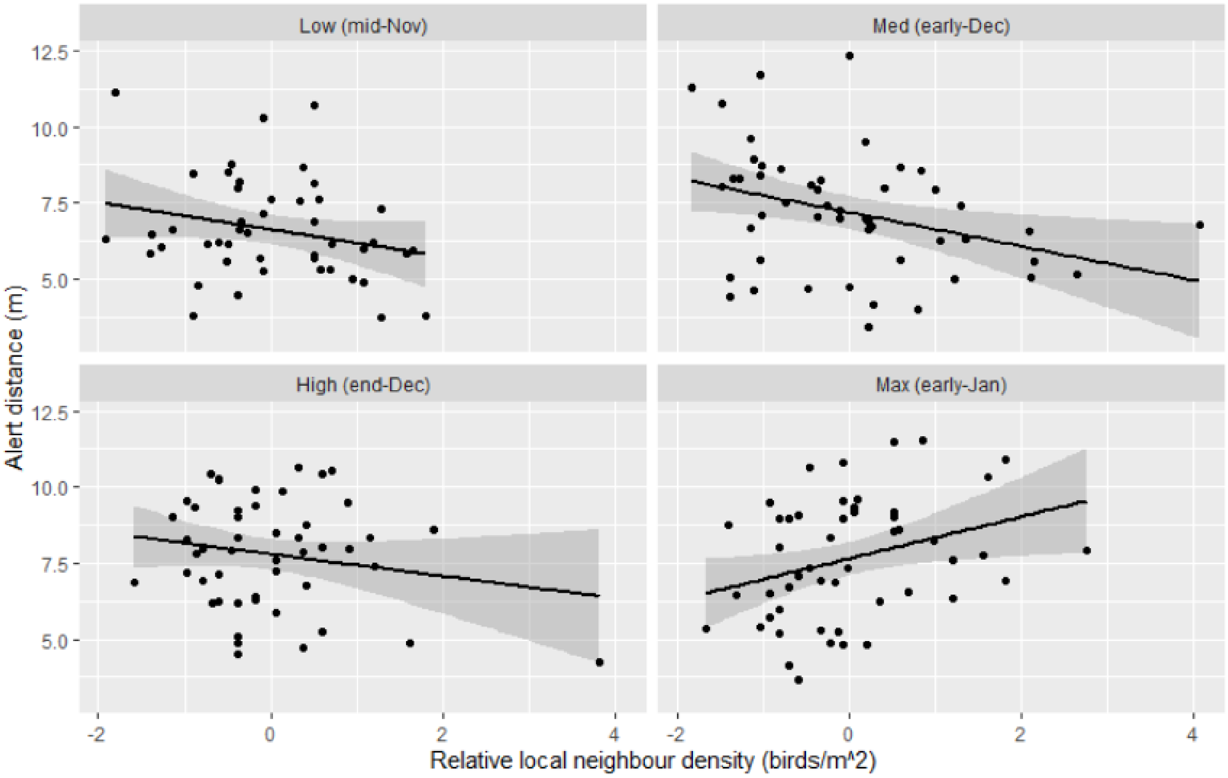

Figure 23. **The significant effect of the interaction between relative local neighbour density (number of birds/m^2) and colony density (low, medium, high, and max) on Alert Distance (AD) is depicted in incubating king penguins (*Aptenodytes patagonicus*).** Dots represent the raw AD values (194 observations); shading represents the 95% confidence interval predicted from the model while holding other variables in the model constant.

Of the 200 individuals approached, 50% did not flee. Focal birds that were more aggressive towards their neighbors during approach were significantly less likely to flee (X^2 = 4.16, P = 0.041). The decision to flee (GLM, N = 193 with complete information), was not explained by relative colony rank (X^2 = 0.00, P = 0.979), relative local neighbor density (X^2 = 1.52, P = 0.218), or overall colony density (X^2 = 1.35, P = 0.717) (Fig. 24).

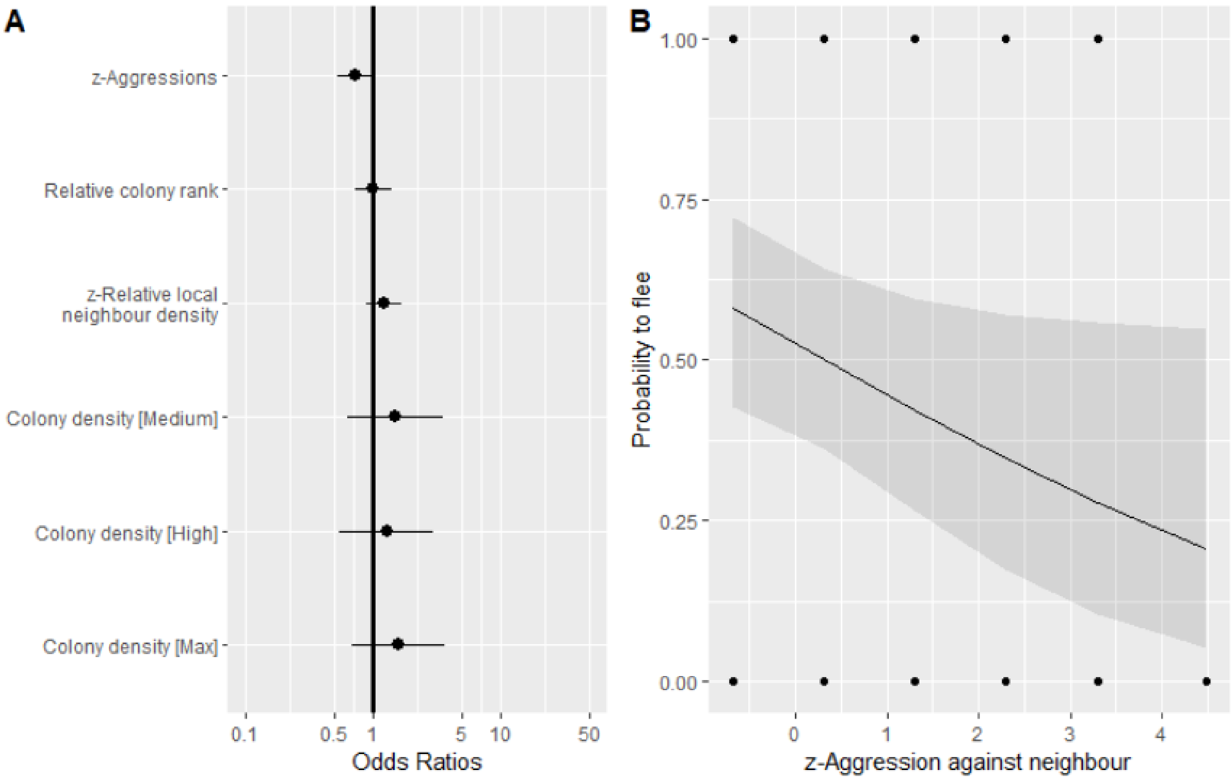

Figure 24. **Variables affected the probability of initiating flight in incubating king penguins (*Aptenodytes patagonicus*).** A) A generalized linear mixed model depicting the decision to flee (binomial; 0 = no flight initiated, 1 = flight initiated). Odds ratios and 95% confidence intervals for the number of aggressions with conspecifics during the approach, relative local neighbour density, and colony density (low, medium, high, and maximum) (n = 193 observations). B) The significant predicted effect between the probability to initiate flight (binomial; 0 = no flight initiated, 1 = flight initiated), and the number of aggressions during the approach against neighbouring individuals by the focal individual. Shading represents the 95% confidence interval predicted from the model while holding other variables in the model constant.

Of the individuals that decided to flee (LMM, N = 93), the mean FID was at 3.00 ± 1.57 m; (range = 0.54 – 8.46 m). Birds showed greater FID when approached at faster speeds between AD and FID ($F_{1,79.8}$ = 20.1, P <0.001) (Fig. 25). Variation in FID was not explained by aggression with neighbors ($F_{1,78.5}$ = 2.45, P = 0.122), relative colony rank ($F_{1,72.0}$ = 0.66, P = 0.418), relative local neighbor density ($F_{1,80.0}$ = 0.52, P = 0.474), or overall colony density ($F_{3,78.7}$ = 1.02, P = 0.390).

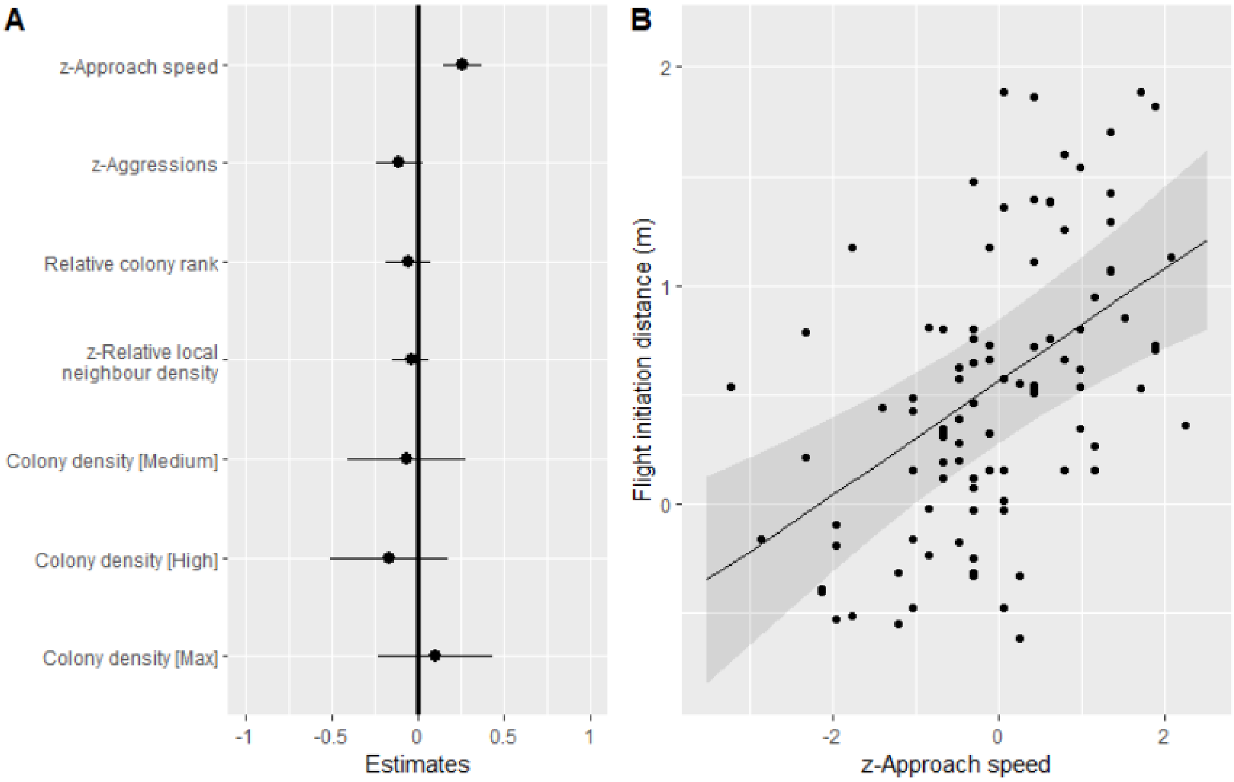

Figure 25. Variables affecting Flight Initiation Distance (FID) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of the number of aggressions against conspecifics, relative local neighbour density, and colony density (low, medium, high, and maximum) (n = 93 observations). B) The significant predicted effect of approach speed on log FID is depicted. Dots represent log FID values; shading represents the 95% confidence interval predicted from the model while holding other variables in the model constant.

DISCUSSION

This study aimed at examining the contribution of the "many-eyes", "dilution effect", "selfish herd", and "distracted prey" hypotheses in shaping prey anti-predator behavior in colonial king penguins. Our results show that at low and medium overall colony density, increasing relative local neighbor density resulted in a decrease in bird Alert Distance (AD) to an approaching experimenter, while at maximum overall colony density, increasing relative local neighbor density resulted in longer AD. These results provide support for the "distracted prey" hypothesis at low colony densities and support for the “many-eyes” hypothesis at maximum colony density. In addition, birds who engaged in aggressive behaviors with their neighbors during the approach were less likely to initiate flight, supporting the “distracted prey” hypothesis. In contrast, bird Flight Initiation Distance (FID) did not appear to vary depending on overall or relative local bird density, nor was it affected by bird aggression or relative colony rank. Our results provide limited evidence in support of a selfish herd effect or risk dilution effect.

To the best of our knowledge, no study has so far investigated all four of these hypotheses simultaneously, especially not in incubating birds, although the “many-eyes” and “dilution effect” hypotheses have been simultaneously studied using both mathematical models (Fairbanks and Dobson 2007; Rieucau and Martin 2008; Beauchamp 2017) and field studies (Boland 2003; Schmitt et al. 2014). For instance, in bighorn sheep (*Ovis canadensis*) foraging ewes were found in predictive models to benefit from both the “many-eyes” and “dilution effect” hypotheses as group size increased (Rieucau and Martin 2008). Similarly, emus (*Dromaius novaehollandiae*) spent less time in vigilance in larger groups, detected approaching threats sooner, and waited longer before initiating flight, supporting both the many-eyes and dilution effect hypotheses (Boland 2003). In Columbian ground squirrels (*Urocitellus columbianus*) a predator detection model was better supported than a dilution model (Fairbanks and Dobson 2007), and in plains zebras (*Equus quagga*), predator detection benefits were found to be more influential in mixed-species groupings than dilution effects (Schmitt et al. 2014). Over 53 published studies, Beauchamp (2017) found the many-eyes and dilution effect hypothesis acted together to reduce predation risk most often in species that form groupings. These studies serve to emphasize the point that hypotheses in relation to group size on prey reactions to approaching predators and other environmental (social) stimuli are not mutually exclusive and may frequently work in concert (Roberts 1996). Yet, whereas the “many-eyes” and “dilution effect” hypotheses have been considered together in past studies, the inclusion of the “distracted prey” or “selfish herd” hypotheses in understanding prey reactions remains an open question. Although these hypotheses have not been considered conjointly, all but the “distracted prey” hypothesis have been tested individual in starlings, *Sturnus vulgaris* (Zoratto et al. 2009). They have been shown in larger groups to decrease individual vigilance yet respond faster to the approach of a model predator (“many-eyes”, Powell 1974), form larger flocks when predation risk is high (“dilution effect”, Carere et al. 2009), and individuals show higher rates of vigilance and decreased foraging rate when on the periphery of the group (“selfish herd”, Jennings and Evans 1980). When considered alone, the “selfish herd” hypothesis has mixed support in the field (for mathematical support see: Reluga and Viscido 2005; Morrell et al. 2011), with some studies supporting individual risk minimization by selfish attraction to other members when under attack (sheep, King et al. 2012; fish, Krause 1993; crabs, Viscido and Wethey 2002), and other failing to detect such effects (fish, Parrish 1989; birds, Sankey et al. 2021).

Of the four hypotheses (“many-eyes”, “dilution effect”, “selfish herd”, and “distracted prey”), only the “many-eyes”, “selfish herd”, and “distracted prey” hypotheses imply changes in the vigilance effort. In the “many-eyes” hypothesis, larger and/or denser groupings contain more individuals that can contribute to group-vigilance at any point in time, leading to an increase in AD. Indeed, AD is expected to be longer when the focal individual is investing more into vigilance behavior, surveying its surroundings, thus being able to detect approaching threats sooner (Fernández-Juricic and Schroeder 2003; Beauchamp 2015; Uchida et al. 2019); but see Tätte et al. 2019). According to the “selfish herd” hypothesis, individuals in the periphery who are less protected by conspecifics face the highest predation risk and should therefore have the highest vigilance (hence highest AD). In contrast, the “distracted prey” hypothesis predicts that external stimuli may distract from vigilance behavior, leading to shorter AD. At low and medium colony densities, we observed that incubating adult king penguins show a decrease in AD as relative local neighbor density increased supporting the “distracted prey” hypothesis. However, at maximal colony density AD increased with relative local neighbor density, consistent with the “many-eyes” hypothesis. Earlier in the breeding season (at low colony density) king penguin breeding pairs establish their territories within the colony (Stonehouse 1960; Weimerskirch et al. 1992; Viblanc, Saraux, et al. 2014). The social aggression that occurs during territory establishment and the resulting colony instability at that time (Viblanc, Saraux, et al. 2014) may distract individual birds from surveying for predators. These results are consistent with reports from other species. For instance, in a study that surveyed both a South American cichlid fish, *Nannacara anomala*, and the willow warbler, *Phylloscopus trochilus*, male-male conflicts reduced vigilance behavior and resulted in a delay of predator detection when shown the image of a predator (Jakobsson et al. 1995) A similar result was found in another cichlid species, *Neolamprologus pulcher* (Hess et al. 2016). Similarly, European robins, *Erithacus rubecula*, were significantly slower to react to a stuffed sparrowhawk when engaged in territorial defense (Dunn et al. 2004). Later in the breeding season (at maximum colony density), king penguins are already settled into their territories and colony density is relatively stable (Viblanc, Saraux, et al. 2014). At high density, the information about disturbances may disseminate rapidly from neighbor to neighbor and may aid in searching for and detecting predators (a ripple of disturbance is caused by entering the colony, which alerts neighboring individuals of approaching threats, TLH, VAV, PB *pers. obs*.) (see also Hernández-Matías et al. 2003). Hence, at low colony densities, the distraction hypothesis appears supported, but at high colony densities the many eyes hypothesis is supported. Furthermore, those results may be amplified in concert with predation pressure on the eggs of incubating king penguins which varies across the breeding season. Indeed, previous studies show that predation pressure increases over the breeding season (Descamps et al. 2005). With low predation pressure and low colony density at the start of the breeding season, breeding king penguins may be more attentive to their social environment than to predators. In contrast, with higher predation pressure later in the season when the colony is at its peak density, breeders would shift their attention more towards predators and antipredator responses than to their peers (Descamps et al. 2005).

In contrast to AD, bird Flight Initiation Distance (FID) is expected to vary with the “dilution effect”, “distracted prey” and “selfish herd” hypotheses. All hypotheses predict similar responses in terms of FID. FID is the result of a decision-making process that occurs after a predator is detected. On one hand, as the number of individuals within a group increases, individual predation risk decreases, and therefore FID should be reduced (“dilution effect” hypothesis). On the other hand, as the number of individuals increases, so does the number of social distractions (e.g., aggression between neighbors), which in turn should distract the focal individuals from performing the necessary decisions needed to initiate flight at an appropriate time, causing FID to be delayed. In the “selfish herd” hypothesis, central positions face reduced predation risk, and the colony is more densely packed, and should therefore have shorter FID. Yet, FID was not impacted by relative local neighbor density, overall colony density, rank, or aggression with neighbors in incubating king penguins, and therefore neither hypothesis appeared to be strongly supported. One potential explanation to this result may have to do with the cost of reproduction shaping optimal flight initiation distances (Cooper and Frederick 2007). In king penguins, truly fleeing from an approaching predator means abandoning the egg/chick and losing reproduction for the year. Most often, flight is attempted by attempting to slowly move away with the egg or young chick on top of the feet – an action that is obviously mechanically constrained. In addition, even attempting to slowly move away with the egg or young chick may trigger aggressive responses from neighboring conspecifics and increase the risk of injuries and damage to the egg. Indeed, the commitment to reproduction is especially high in king penguins, as it takes the cooperation of a breeding pair for over 14 months to raise a single chick, and successful reproduction occurs at best every two years (Jiguet and Jouventin 1999). Thus, there may be strong selection in this species for behaviors aimed at the early detection of approaching threats and for active territory defense (Côté 2000) despite risks of injury, rather than fleeing altogether from approaching predators, given the elevated fitness costs of abandoning reproduction. FID may then be a relatively inflexible trait in breeding individuals of this species and therefore dilution or distraction effects on this trait may be small. Our previous study found that FID and the decision to flee were significantly repeatable, highlighting moderate to strong individual components in incubating king penguins (Hammer et al. 2022). It is perhaps then not surprising that personality traits were not significantly affected by the social environment, whereas AD, a trait found to be highly flexible and lowly repeatable (Hammer et al. 2022), was.

We found that the decision to initiate flight in this species was significantly reduced when the focal bird was engaged in social aggression with neighboring conspecifics, a result which supports the "distracted prey" hypothesis. In this species, territorial defense of incubation and brooding territories is high (Côté 2000), and the "distracted prey" hypothesis suggests that time spent processing social cues and engaging in social interactions with conspecifics may undermine the ability to perform anti-predator behaviors such as vigilance and flight (Chan et al. 2010). It appears that for king penguins, social aggression may be a strong distraction from the ability to decide when to initiate flight. Although previous studies have not considered how social aggression may affect individual responses to approaching predators, allogrooming impala, *Aepyceros melampus*, had reduced vigilance rates and responded on average 4 seconds later to a simulated predator than non-allogrooming individuals (Mooring and Hart 1995). Anoles, *Anolis sagrei*, when presented with a conspecific tolerated closer approachers of a model predator before initiating flight (Yee et al. 2013). Of particular interest is that territorial defense, such is seen in king penguins, is particularly distracting for focal individuals (as discussed above). For example, in a South American cichlid fish, *Nannacara anomala*, individuals engaged in territorial mouth wrestling showed reduced vigilance, and chose low intensity behaviors such as display and tail beating when in the presence of a model predator (Brick 1998).

Studies have typically focused on prey behavioral responses to predators in the context of foraging (e.g., Fernández et al. 2003; Randler 2005; Fairbanks and Dobson 2007; Rieucau and Martin 2008; Taraborelli 2008; Schmitt et al. 2014). In contrast, our study focused on the existence of a trade-off between vigilance and flight behavior depending on the individual perceptions of the social and predatory environments in the context of colonial breeding (Williams 1966). Colonial breeding in seabirds has mostly been suggested to emerge as a consequence of the utilization of patchy and unpredictable marine food resources and limited favorable breeding grounds (Clode 1993; Boulinier et al. 1996; Danchin and Wagner 1997; Boulinier et al. 2008). The role predation plays in its evolution, however, remains unclear (Rolland et al. 1998). Several studies have reported antipredator benefits to colonial breeding, by diminishing individual predation risk through dilution, predator-mobbing, or selfish herd effects (Brown and Brown 1987; Picman et al. 2002; Hoogland and Sherman 2012). Our results are consistent with apparent anti-predator benefits of colonial breeding which comes in the form of shared vigilance and predator detectability, but that are traded-off with costs and loss of predator detectability due to social distractions.

Although our present study provided little support for selfish herd effects in king penguins, observations in the field show that birds subject to an experimental reduction in local breeding density (by means of exclosure pens) cluster closer together rather than use the available freed-up space (Viblanc 2011), consistent with the selfish herd notion of minimizing individual predation risk. Clustering close to conspecifics combined with the high territorial and aggressive behavior of king penguins (Côté 2000) results in producing a tightly woven network or aggressive birds, making it hard for predators to land in the middle of the colony (TLH, PB, BG, JPR, RG, VAV; personal observation). Of interest is the idea that breeding aggregations in penguins result from a combination of self-organized dynamics related to predation risk (selfish herd effects) and external forcing factors such as topographically limited possibilities of spatial re-arrangement, for instance due to the retainment of nesting sites year after year (e.g., in Adélie penguins, *Pygoscelis adeliae*, McDowall and Lynch 2019). This may result in trapping individuals into suboptimal spatial arrangements, with strong edge effects (McDowall and Lynch 2019; Schmidt et al. 2021). King penguins incubate their single egg on their feet, hence, virtually nothing is known on how closely individuals retain breeding sites year after year, nor whether variation in individual's ability to maintain a breeding site may lead to a situation of entrapment into suboptimal conditions. Future studies should aim at understanding how the "dilution effect", "many-eyes", "selfish herd", and "distracted prey" hypotheses are shaped not only by social and predatory environments, but in interaction with local topography and individual quality. In addition, nothing is known on how such interactions might be shaped by residual reproductive value. For instance, studies in seabirds have found that older parents for which residual reproductive value is low are less responsive to stressors (Heidinger et al. 2006, 2010, but see Elliott et al. 2014). It would thus be of interest to understand how age and residual reproductive values factor into affecting physiological stress responses in addition to behavior in shaping antipredator decisions.

While overall colony density increases as the breeding season progresses, reproductive investment of the breeding individuals also changes with advancing breeding season. Two factors might affect the responses of incubating birds sampled early or late in the breeding season. First, birds that entered reproduction early in the season come nearer to hatching as the breeding season progresses, and hence reproductive investment should increase. It is likely that, as reproductive investment increases, protecting the investment (i.e., deciding to not flee, or to flee later from an approaching threat) may weigh more heavily on anti-predator behavior (Clark and Ydenberg 1990). Second, birds sampled later in the season may be late breeding birds just starting their incubation. Late breeders in king penguins rarely, if ever, succeed, as chicks are most likely to die before or over winter (Stonehouse 1960; Weimerskirch et al. 1992; Stier et al. 2014). In turn, the lower value of reproduction later in the season may render individuals less willing to defend their brood and more likely to flee. Unfortunately, not knowing the incubation stage of birds in our study, we were unable to differentiate responses under those different scenarios. Thus, future studies are needed to specifically test anti-predator responses linked to reproductive value and breeding advancement. While we did not see a change in FID or a change in the probability of initiating flight as the breeding season progressed, there remains a link between reproductive success, brood investment, and risk assessment in later breeding birds that needs to be explored in more depth. For instance, focusing on physiological stress responses (e.g., heart rate known to vary with advancing breeding season; Viblanc et al. 2015) in addition to behavioral responses to approaching predators may yield some valuable information (Viblanc et al. 2015).

To conclude, our study found that the “many-eyes” hypothesis was supported at maximum colony density, while the “distracted prey” hypothesis was supported at lower colony densities in incubating king penguins. In addition, focal birds that were engaged in social aggression with neighboring conspecifics were less likely to initiate flight. We found little support for the “selfish herd” hypothesis based on bird centrality in the colony, and no evidence that the dilution effect was strongly influential. These results show that prey behavioral decisions towards approaching threats are complex, and likely explained by a mix of mutually non-exclusive hypotheses. Future studies on prey reactions to predators should consider testing for joint effects of environmental and social factors in understanding risk-benefit assessments in wild animals.

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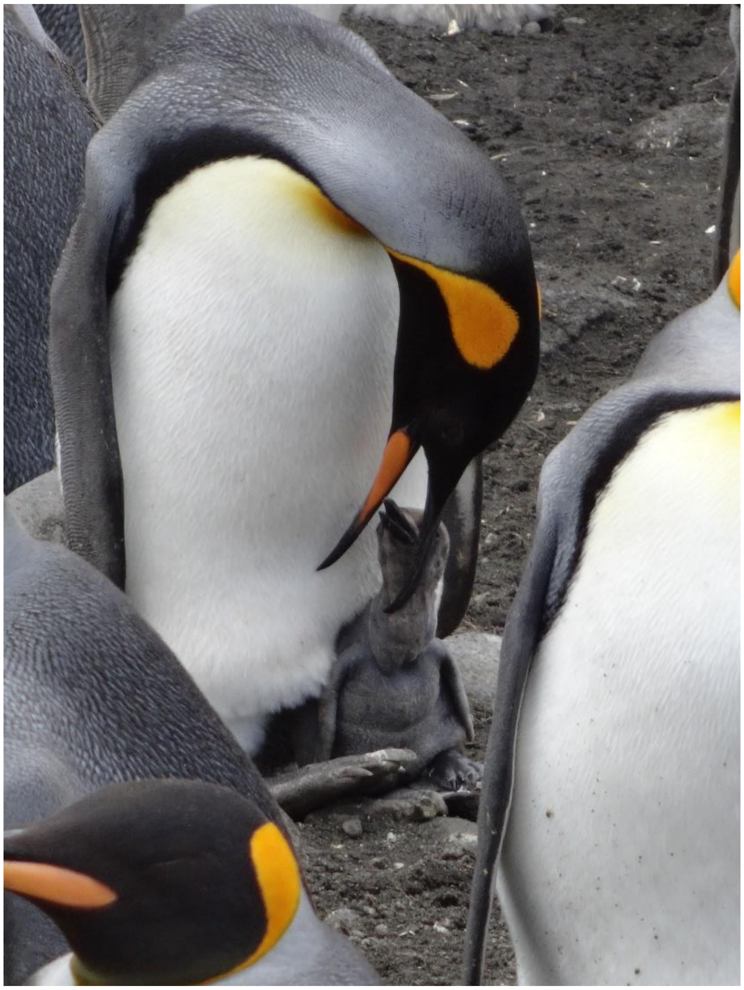
Chapter 3



Effect of the trade-off between current and residual fitness on alert and flight initiation distances in king penguins (*Aptenodytes patagonicus*)

Tracey L Hammer[1], Pierre Bize[2], Benoit Gineste[1,3], Jean-Patrice Robin[1], René Groscolas[1], Vincent A Viblanc[1]

[1]University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000 Strasbourg, France

[2] Director of Research, Vogelwarte, Sempach, Switzerland

[3]IPEV – Institut Polaire Français Paul Émile Victor, 29280 Plouzané, France

ABSTRACT

When approached by predators, prey must decide whether to flee or remain and fight. The economics of such decisions are underlain by the trade-off between current and residual fitness. It predicts that (i) breeders should be less prone than non-breeders to flee from approaching predators, as breeders can potential successes in current reproduction; (ii) among breeders, parents should increasingly defend their offspring with increasing investment into the brood (brood value hypothesis), at least until the offspring can independently take part in anti-predator defenses; (iii) for a similar investment into reproduction, breeders with lower perspectives to fledge or wean their young should invest less into offspring defense. We tested these predictions in a colonially breeding seabird, the king penguin (Aptenodytes patagonicus). Specifically, we considered how antipredator behaviors varied according to life history stage (molting, courting, breeding), offspring age, and dependence on their parents for antipredator defenses, and the timing of breeding which strongly influences the likelihood of successful reproduction in this species. Using non-lethal human approaches to mimic the threat of predation, we approached >400 penguins and measured their Alert (AD) and Flight Initiation (FID) Distances, as well as the Distance Fled (DF). We found that birds show increasingly stronger antipredator behaviors as they initiate and increase their investment into reproduction, from non-reproductive stages to courting and brooding small, thermo-dependent chicks, before reducing their antipredator behaviors after their offspring gained thermo-independence and freedom of movement. Late breeders were more likely to flee from the approaching threat than early breeders. Altogether, our results demonstrate that parental antipredator responses are dynamic and shaped by the current investment into reproduction, the ability of offspring to defend themselves, and the perceived future value of the brood.

282/300 words

Key words: predation risk, escape-flight distance, risk taking, stress, life-history trade-off

INTRODUCTION

When faced with approaching predators, prey must undertake decisions on whether to flee or not, and if they do, how close to allow predators to approach before initiating flight. Flight Initiation Distance (FID) is thus an estimation of the amount of risk a prey evaluates as acceptable (Ydenberg and Dill 1986). If the risk is perceived to be high, prey should initiate flight sooner, for example, when a predator displays higher intent in the approach, such as approaching quickly (Cooper 1997; Cooper et al. 2003; Stankowich and Blumstein 2005; Cooper and Whiting 2007; Bateman and Fleming 2011) or directly (Burger and Gochfeld 1990; Cooper 2003; Cooper et al. 2003; Smith-Castro and Rodewald 2010). However, it is not just the level of risk that determines when prey will initiate flight. Optimal escape distances are shaped by a trade-off between the fitness gains acquired from flight behavior vs. the fitness losses incurred by abandoning the current activity in which the individual is engaged at the time of predator disturbance (Cooper and Frederick 2007). Not only can fleeing interrupt self-care and foraging activities, it may further interfere with breeding activities including territory establishment and defense (Jakobsson et al. 1995; Dunn et al. 2004; Møller et al. 2008; Hess et al. 2016), pairing and mate choice (Cooper and Wilson 2007; Cooper 2009; Ventura et al. 2021), nest building (Lima 2009), or offspring care (Montgomerie and Weatherhead 1988; Carter et al. 2009; Arroyo et al. 2017; Novčić and Parača 2022). When fleeing interrupts a fitness enhancing behavior, the best course of action may be to delay flight as long as possible.

For breeding adults, the decision to stay and protect their young against a predator, potentially risking serious injuries or death, or to flee and abandon reproduction altogether, is conditioned by a trade-off between the value of current reproduction vs. that of future breeding opportunities (Williams 1966; Trivers 1972; Montgomerie and Weatherhead 1988). Parental commitment to offspring is expected to increase, and FID decrease, as the relative reproductive value off the offspring increases (the “brood value hypothesis”) (de Jong et al. 2013; Arroyo et al. 2017), and if the chances of offspring survival to sexual maturity is high (Trivers 1972). As offspring age, their likelihood of survival to independence increases, and parents will invest more resources (time and energy) in raising them, leading to higher offspring value (Barash 1975; Andersson et al. 1980; Ackerman and Eadie 2003; Redmond et al. 2009; Svagelj et al. 2012). In addition, in many species, the ability to reproduce successfully a second time within a breeding season declines as the breeding season advances due a drastic reduction in the chance of successfully raising a brood to fledging, and so the cost of losing offspring to predation increases (Andersson et al. 1980; Montgomerie and Weatherhead 1988; Redmond et al. 2009). Accordingly, in birds, studies have suggested that in species with high re-nesting potential, parents should commit less effort to nest defense and have longer FIDs than those with low re-nesting potential (Dawkins and Carlisle 1976; Boucher 1977; Weatherhead 1979; Klvaňová et al. 2011; Svagelj et al. 2012). Alternatively, in many other species, the likelihood for parents to fledge or wean their offspring drastically declines as the breeding season advances, and thus late breeding parents should be less prone to defend their brood against predators. Thus, offspring of higher reproductive value should be those that are older, or those that are impossible to replace due to the advancement of the breeding season, or those that, independently of their age, are more likely to reach maturity due to the advancement of the breeding season (Barash 1975; Andersson et al. 1980; Kleindorfer et al. 1996; Tryjanowski and Goławski 2004).

Beside offspring age and the advancement of the breeding season, parental investment into offspring defense is also known to peak depending on the intersection of highest brood vulnerability and highest brood value (which occurs at hatching/birth or at fledging/weaning, depending on the species) (Barash 1975; Andersson et al. 1980. The dependence of offspring upon their parents for protection against predators (contingent on whether offspring are both altricial or precocial) appears to play an important role in shaping parental responses to predators). In species with precocial young, parental defense of offspring is usually highest immediately after hatching/birth and declines quickly as offspring near fledging/weaning and gain the physical independence necessary to flee predators on their own (killdeer, *Charadrius vociferus*, Brunton 1990; willow ptarmigan, *Lagopus lagopus*, Sandercock 1994;

Savanna nightjar, *Caprimulgus affinis*, Tseng et al. 2017). In species with altricial offspring, parental investment in offspring defense continues to increase with offspring age, peaking later in the nestling phase prior to fledging/weaning when offspring begin to develop some independence in movement (fieldfare, *Turdus pilaris*, Andersson et al. 1980; Adélie Penguins, *Pugoscelis adeliae*, Wilson et al. 1991; meadow pipit, *Anthus pratensis*, Pavel 2006; African penguin, *Spheniscus demersus*, Pichegru et al. 2016). In bird species with altricial young, interruptions of parental care shortly after hatching (when altricial chicks heavily rely on parents for brooding), may also greatly increase the risk of nest failure. Parents of altricial chicks may thus be less willing to flee the nest upon the approach of a predator than in species with precocial young, whose offspring are frequently observed scattering upon the approach of a predator and might survive independently of the parent for a period of time (Andersson et al. 1980; Buitron 1983; Sandercock 1994).

Here, using non-lethal human approaches to mimic predation threat (Frid and Dill 2002; Beale and Monaghan 2004, see Hammer et al. 2022 for an example on king penguins), we tested, in a semi-altricial species, the king penguin (Aptenodytes patagonicus), how adults' antipredator responses varied according to their life history stages and their investment into reproduction (molting, courting, incubating, brooding small vs. large chicks), the dependence of their offspring for protection, and their timing of reproduction (early vs. late breeders). King penguins are an interesting model to compare the fitness benefits vs. costs of flight between various life history stages, and more specifically investigate how flight responses or nest defense are shaped by the reproductive value of the brood. Successfully breeding king penguins only produce one egg every 14-16 months (i.e., the time needed to form a pair, lay a single egg, incubate, fledge the chick, and molt before subsequent reproduction) (Stonehouse 1960; Weimerskirch et al. 1992), and therefore the reproductive investment in each egg/chick is extremely high. Only adults that breed in the first half of the reproductive season (i.e. early breeders) are usually successful at fledging a chick (Weimerskirch et al. 1992), since late breeders are constrained by the arriving winter and their breeding success is virtually null (Van Heezik et al. 1994; Olsson 1996). Thus, re-nesting potential is extremely low in this species. Therefore, the relative value of the brood is expected to be higher for early breeding birds (Barash 1975; Andersson et al. 1980; Montgomerie and Weatherhead 1988; Redmond et al. 2009). The chicks are hatched in a semi-altricial state and remain highly dependent on their parents for feeding, protection, and body heat for the first thirty days. After one month they are able to achieve thermal independence when they grow in a coat of down (Stonehouse 1960). At this age, the chicks become less reliant on parental care as they can cluster into "creches", decreasing their risk of predation without necessary protection of their parents (Stonehouse 1960; Le Bohec et al. 2005). Breeding king penguins are also highly aggressive, and territorial aggression increases upon the hatching of a chick, reflecting increased brood defense (Côté 2000).

We approached >400 individual penguins at different life history stages and measured their behavioral reaction to our approach, including the distances at which they detect the approach (Alert Distance, AD), the distance at which they initiated flight (FID), and the distance over which they fled once flight occurred (Distance Fled, DF). We also recorded the number of aggressive interactions emitted towards the approaching experimenter. According to life history theory on the tradeoff between current and residual fitness (Roff 1992; Stearns 1992), we predicted that (i) breeders should be less prone than non-breeders to flee from approaching predators as breeders can lost their investment into current reproduction; (ii) among breeders, parents should invest more into offspring defense and be less prone to flee with increasing investment into the brood as offspring age (brood value hypothesis), at least until the offspring can somehow also take part in anti-predator defenses (Le Bohec et al. 2005); (iii) for a similar investment into reproduction, breeders with lower likelihood to fledge their young should invest less into offspring defense (i.e. late breeders vs. early breeders).

To test these predictions, we first compared bird behavioral reactions across a range of life history stages committed to reproductive activities (courting birds, birds in breeding pairs, incubating birds, and brooding birds), or not (molting birds, and non-breeders). We expected birds in breeding pairs to have shorter FID and DF and to be more aggressive than molting birds and birds not engaged in reproductive activities. We further expected birds with eggs and chicks to have the shortest FID and DF, to be less likely to initiate flight, and to be the most aggressive due to their increased reproductive investment.

We then compared the response of parents rearing chicks of different ages (less or more than 30 days old, see methods). We expected to find higher nest defense and shorter flight responses in birds caring for young chicks which are of higher reproductive value than eggs, and in early breeding birds for which the likelihood of successful reproduction is higher. Increasing parental offspring defense and decreasing flight behavior from hatching to early brooding stages when chicks are the most vulnerable and reproductive value highest, followed by a subsequent decrease in chick defenses and increase in flight behavior once chicks gain physical autonomy (and are able to flee from predators independently).

Finally, we tested for differences in parental commitment to reproduction between early and late breeding adults, since in this species only early breeding adults (during the first half of the reproductive season) have a reasonable chance of successfully raising a chick (Weimerskirch et al. 1992; Van Heezik et al. 1994; Olsson 1996). We expect late breeders to be less willing to invest into offspring defense and show longer FID and DF, and increased susceptibility to initiate flight upon the approach of an experimenter.

METHODS

Study site and animals

This study was conducted during the 2010-2011 and 2011-2012 austral summers in the king penguin colony of “La Baie du Marin” (22 000 breeding pairs, Barbraud et al. 2020) located in the Crozet Archipelago (Possession Island, 46°25’S – 51°52’E).

In the first analysis, in an investigation of how birds reacted to an approaching threat at various life history stages and to further test the brood value hypothesis among the breeding adults, we approached 467 adult king penguins. Individual birds were either molting birds (N = 26), not engaged in reproduction (N = 24), courting (N = 20), settled on their final breeding territory with their partner, i.e., in breeding pairs (N = 17), incubating (N = 252), brooding small, thermally dependent chicks (TDC; <30-days old) (N = 78), or older, thermally independent chicks (TIC; >30-days old) (N = 50). TDC depend on their parents for thermoregulation and are kept warm against the adult in the brood pouch until they have grown a full set of down feathers and are able to be left alone for longer periods while the adults forage at sea. All breeding birds measured in this section were early breeding birds. In the second analysis, to test how breeding prospectives affected antipredator behavioral reactions to an approaching threat, we compared the behavior of an additional set of birds that were incubating early (November, N=50) to birds that were incubating late (March, N=50) in the breeding season. Individuals were chosen at random: we have no information on their age and sex, nor the exact laying dates and shift for all incubating and brooding birds.

Approach protocol

All approaches occurred between 8:00 am and 6:00 pm and were carried out by the same observer (B.G.) wearing the same clothing for each approach. Approaches were only started in clear sight of the target animal when the animal was at rest (not engaged in aggressive, grooming, sleep, courting, or offspring care). All aggression directed towards the approaching experimenter during the approach was recorded in order to measure territoriality and brood defense (see below). All occurrences of threats and physical blows towards the experimenter were counted. Aggression during approach for birds in breeding pairs was not recorded. Distances between the observer and the focal bird were measured using a laser telemeter (Leica DISTO^{TM} D5 Lasermeter, Leica Geosystems AG, Hexagon, Sweden). For most approaches (465/567, 82%), start distances were standardized to 18 m to control for the commonly observed effect that start distance has on AD and FID (Dumont et al. 2015; Blumstein, 2010; Blumstein, 2003); however, not all start distances could be standardized. Courting birds and birds in breeding pairs were approached between 12 m and 20 m (mean 14.3 m and 13.8 m, respectively), and some incubators between 11 m and 20 m (mean 17.8 m) despite most being standardized at 18m (313/352, 89%). The starting distance for brooders of TDC varied between 16 m and 18 m (mean 17.8 m). A preliminary analysis showed no relationship between starting distance and AD or FID within any of the breeding stages (AD: courting birds, r_{20} = 0.25, P = 0.29, birds in breeding pairs, r_{17} = 0.11, P = 0.67, incubating birds, r_{252} = 0.09, P = 0.16, brooders of TDC, r_{78} = 0.11, P = 0.35; FID: courting birds, r_{20} = 0.12, P = 0.60, birds in breeding pairs, r_{17} = -0.10, P = 0.72, incubating birds, r_{119} = 0.12, P = 0.20, brooders of TDC, r_{41} = -0.29, P = 0.06), so we did not control for starting distance in later analyses. Approaches followed a direct trajectory, with the observer walking at a regular speed until the occurrence of AD (observable due to movement of the focal animal's head in the direction of the experimenter), and FID (when the target animal initiated an attempt to flee). At these two times, the experimenter took a standardized one-minute pause to record information. Animals were approached until close contact. If flight occurred after close contact, the distance at which the focal animal fled (DF) was recorded. Because some birds did not systematically flee upon approach until close contact (FID=0), FID was considered in two different sets of analyses. The first explored the decision to initiate flight as a binary variable (0/1; no flight/flight), and the second explored FID in those animals that choose to initiate flight prior to close contact.

We calculated speed of approach in three separate periods: the speed of approach prior to AD (mean ± SE; 0.57 ±0.11 m/s, range = 0.27 – 1.23 m/s), the speed of approach prior to FID (0.48 ± 0.12 m/s, range = 0.03 – 1.06 m/s), and the speed of approach prior to contact (0.46 ± 0.13 m/s, range = 0.13 – 0.83 m/s). In addition, we systematically recorded weather conditions before each approach to control for potential effects of climate conditions on bird behavior. Air temperature was measured to the nearest 1°C and the levels of wind and rain were scored between 0 (none) and 2 (strong or heavy) with intermediate levels (0.5) being permitted.

Statistical analyses

We used separate mixed effects models with appropriate error distributions (Linear Mixed Models, LMM, or Generalized Linear Mixed Models, GLMM; package “lme4’ in R Bates et al. 2015) to test how AD, FID, the decision to flee (binomial, 0/1), DF and bird aggression towards the experimenter (0/1) were shaped by (1) life history stages (molting, birds not engaged in reproductive activities, courting birds, birds in breeding pairs, incubating birds, birds brooding TDC, and birds brooding TIC); and (2) reproductive timing (early vs. late incubators). Because AD, FID, , and aggressive behaviors can also be influenced by external factors such as the speed of approach (stronger responses in response to faster approaches; Bateman and Fleming 2011; Samia et al. 2016; Hammer et al. 2022), time of day, time of day^2 (predators are often more active at dawn and dusk, leading to stronger responses in the target prey; Petelle et al. 2013; Piratelli et al. 2015; Ferguson et al. 2019), and weather (rain, wind, and temperature) conditions (Couchoux and Cresswell 2012; Hammer et al. 2022), we controlled for these potential effects in our starting models. These factors were then removed sequentially from the final models if they did not explain significant amounts of variation to present the most parsimonious models.

An additional model was used to test the relationship between aggression emitted by the focal bird towards the approaching experimenter and the decision to flee. This last model only included both early and late incubators and brooders of TIC, as they were the only reproductive stages to emit a comparable amount of aggression (required to meet the assumption of homoscedasticity). Because a previous study found that physical blows were 3.2 times more costly in terms of energy expenditure than threat behavior (Viera et al. 2011), we multiplied physical blows (flipper blows and pecking) by 3.2 in order to weigh these behaviors more heavily than threat behaviors (gapping and bill pointing), thus better capturing parental commitment and energy expenditure into brood defense.

In all models, bird location in the colony was included as random factor to control for individuals being measured in similar areas and to account for potential spatial differences (e.g. in landscape, human disturbances, parasites) that could have affected bird behaviors. We removed colony location from models which did not converge due to low amounts of variation explained by this factor, resorting to simpler (generalized) linear models (LM or GLM). This concerned models on: the decision to flee compared between early and late breeders, FID compared between early and late breeders, and DF compared between early and late breeders.

All statistical analyses were performed in R 1.4.1106 (R Development Core Team 2021). Results are presented as means ± SE. Models were run using the package lme4 functions *lmer* and *glmer* (Bates et al. 2015). In models with a gaussian distribution, the significance of fixed effects was tested with the function *anova* from the package lmerTest (Kuznetsova et al. 2017), which utilizes F tests with Satterthwaite estimation for the denominator degree of freedom. For models with a binomial distribution, the function *Anova* was used, which utilizes Wald chi-square tests to test the significance of fixed effects. The package emmeans (Lenth 2021) was used for post-hoc comparisons using the Kenward-Roger degree of freedom method and Tukey method for p-value adjustment. Variance Inflation Factors (VIF) were used to test for collinearity of all independent variables according to Zuur et al. (2010) with a cut off of less than three. These analyses showed that, in the early/late breeder models, temperature was collinear with reproductive stage (weather was warmer later in the season when late breeders were breeding), so we excluded temperature from those models. All variables were scaled and centered prior to inclusion in the models to facilitate their interpretation (Schielzeth, 2010). Where relevant, models were visually checked for the normality of their residuals using “fitdistrplus” (Delignette-Muller and Dutang, 2015), or alternate distributions specified as appropriate (binomial). Although, for one model (comparing DF across life history stages), the residuals were bimodal (the relatively immobile incubators and brooders of TDC vs. more mobile birds from other stages); separating the data into two separate analyses did not significantly alter the results. Thus, for simplicity and clarity, we present model results on DF based on the entire data set, keeping in mind that mixed effects models are robust to deviations from the assumption of normal distributions (Schielzeth et al. 2020). Finally, although we approached a total of 467 individual birds for comparison across the life history stages, and an additional 100 individuals (entirely different from the birds analyzed above) to compare early and late breeders, sample sizes for each model vary due to a lack of complete information for all cases. For example, distances fled were not recorded for many incubating birds (163 of 252 were not recorded), drastically reducing the sample size for this model. Sample sizes for each model are reported in the results.

Ethics statement

No animal was caught or manipulated over the course of this study. The research was approved by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor. Authorizations to enter the colony and approach birds were obtained from Terres Australes et Antarctiques Françaises. The observations complied with the current laws of France. No eggs or chicks were abandoned during the course of this study.

RESULTS

Comparing life history stages

Over all life history stages, individuals became alert on average at a distance of 7.23 ± 2.02 m (mean ± SE, range = 2.18 – 14.7 m, N = 467). Controlling for approach speed prior to AD (LMM, estimate ± SE = -0.21 ± 0.09, $F_{1,438.3}$ = 5.57, *P* = 0.019, N = 448), there were significant differences in AD among the life history stages (LMM, $F_{6,438.0}$ = 7.53, *P*<0.001, N = 448). On average, molting birds had 32.7-39.0%, and non-reproductive birds had 16.2-21.7% higher AD (significant) than the other life history stages (Fig. 26).

In contrast, courting birds, birds in breeding pairs, incubators and brooders did not differ significantly in AD (Fig. 26).

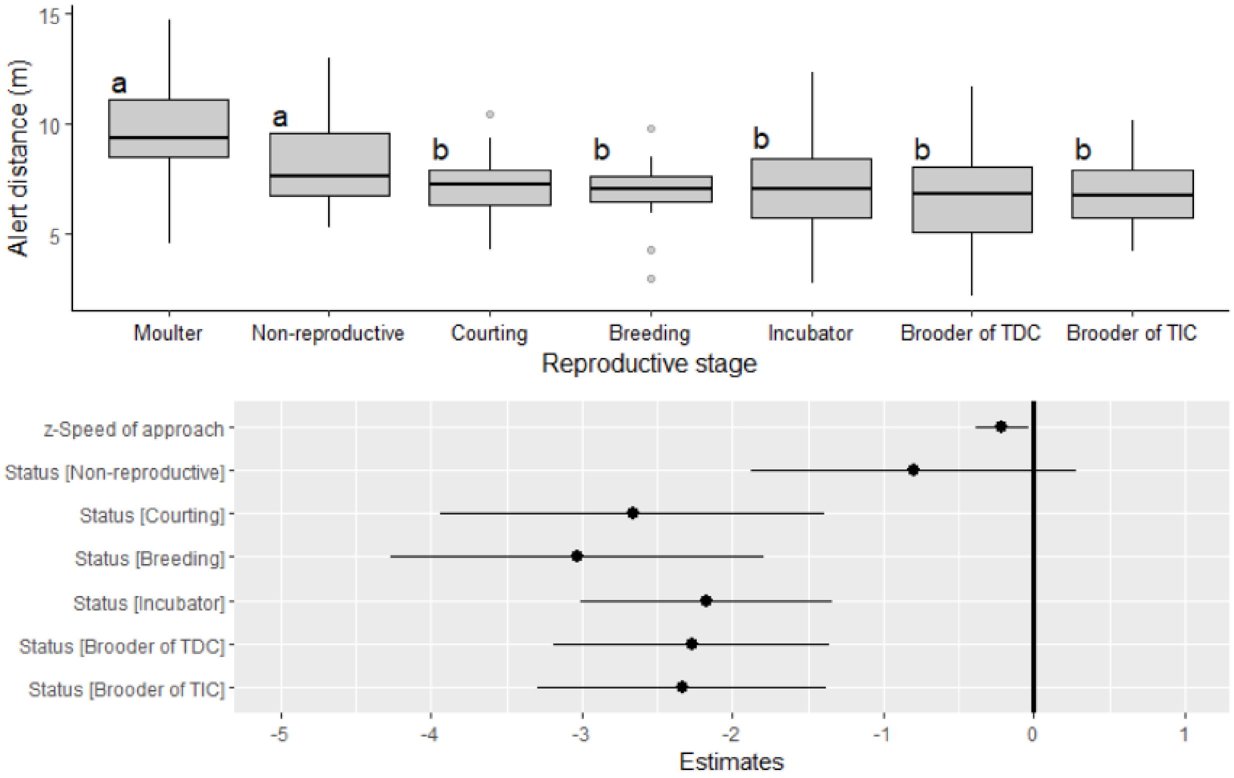


Figure 26. Effect of life history stage on Alert Distance (AD) in the king penguin (*Aptenodytes patagonicus*). (Above) Box and whisker plots of Alert Distances (ADs) observed across different life history stages (N=467). Significant differences between groups were determined using Tukey HSD and are distinguished using the letters a,b. The horizontal bar represents the median, shading represents the interquartile range, and the vertical line represents the 95% confidence interval. (Below) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of speed of approach (scaled and centered), and life history stage on AD.

Incubators initiated flight in 47.2% of approaches (119/252), brooders of TDC in 52.6% of approaches (41/78), brooders of TIC in 94% of approaches (47/50), and all other life history stages initiated flight in 100% of approaches (26/26 molting birds, 24/24 birds not engaged in reproductive activities, 20/20 courting birds, and 17/17 birds in breeding pairs). Focusing on groups for which flight initiation was not 100%, and controlling for approach speed between AD and FID (GLMM, estimate ± SE = -0.39 ± 0.12,

X^2 = 9.34, *P* = 0.002, N = 369), there were significant differences between the life history stages (GLMM, X^2 = 21.7, *P*<0.001, N = 369). Incubators and brooders of TDC did not differ in their probability to initiate flight (Tukey HSD, Z = -1.13, *P* = 0.493), but both fled significantly less often than brooders of TIC (incubator to brooders of TIC: Tukey HSD, *Z* = -4.61, *P*<0.001; brooders of TDC to brooders of TIC: Tukey HSD, *Z* = -3.86, *P*<0.001).

Focusing on the birds that did initiate flight (N = 294), on average and over all life history stages, flight was initiated at a distance of 3.10 ± 2.20 m (range = 0.20 – 14.7 m). Controlling for approach speed between AD and FID (LMM, estimate ± SE = 0.10 ± 0.03, $F_{1,258.4}$ = 8.11, *P* = 0.005, N = 267), there were significant differences in FID between the life history stages (LMM, $F_{6,250.3}$ = 13.5, *P*<0.001, N = 267). On average, molting birds, birds not engaged in reproductive activities, and courting birds had similar FIDs, which were higher than the other stages. That is, on average molting birds had 83.9-206%, non-reproductive birds 58.9-165%, and courting birds 20.9-102% higher FID than other life history stages (Fig. 27). Birds not engaged in reproductive activities, courting birds, birds in breeding pairs, and brooders of TDC and TIC had similar FID, which were significantly higher than incubating birds (non-reproductive had 165%, courting birds 102%, birds in breeding pairs 50.8%, brooders of TDC 64.7%, and brooders of TIC 66.7% higher FID than incubating birds) (Fig. 27). Incubating birds, courting birds, and birds in breeding pairs had the lowest FID compared to all other life history stages (Fig. 27).

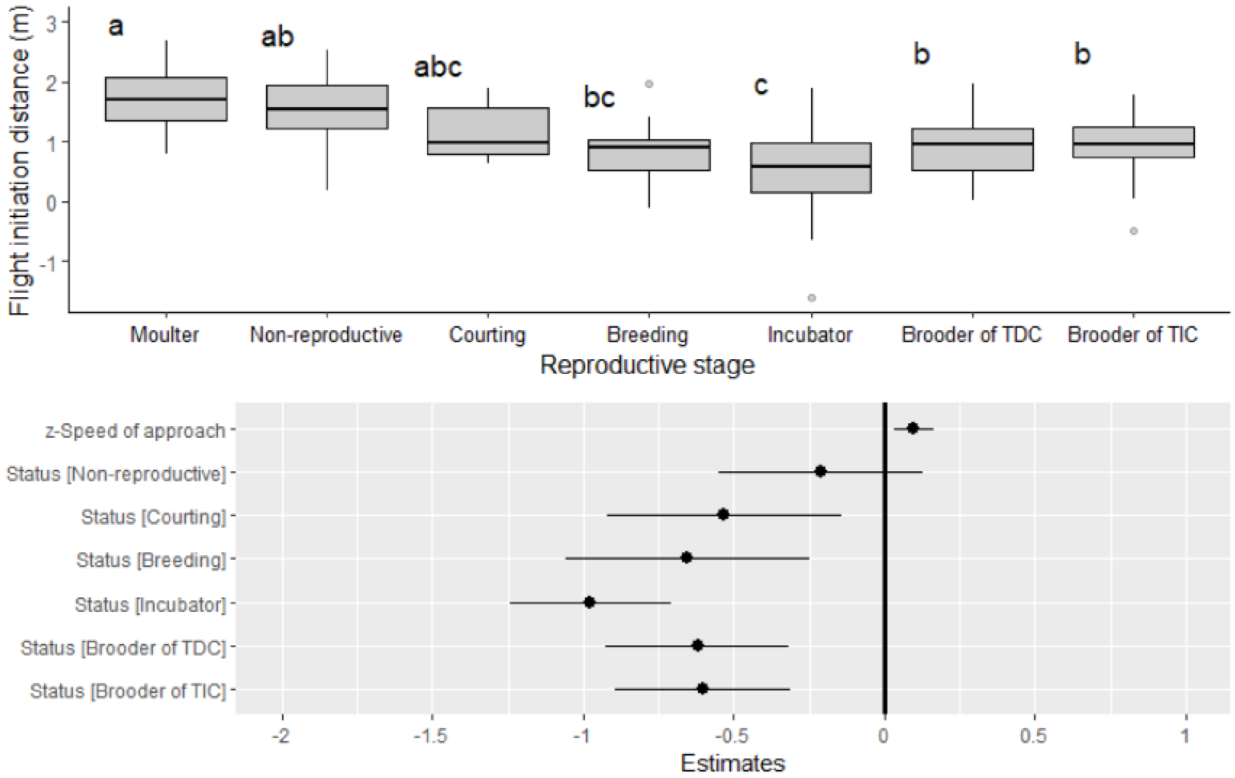


Figure 27. Effect of life history stage on Flight Initiation Distance (FID) in the king penguin (*Aptenodytes patagonicus*). (Above) Box and whisker plots of non-zero FIDs observed across different life history stages (N=294). Significant differences between groups were determined using Tukey HSD and are distinguished using the letters a,b,c. The horizontal bar represents the median, shading represents the interquartile range, and the vertical line represents the 95% confidence interval. (Below) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of speed of approach (scaled and centered), and life history stage on FID.

Across all the life history stages, individuals that decided to flee (N = 201) fled over an average distance of 1.89 ± 2.77 m (range = 0.05 – 15.0 m) from the experimenter after contact. Distance Fled (DF) varied significantly among the life history stages (LMM, $F_{6,172.1} = 136.8$, $P<0.001$, N = 190). Molting birds and birds not engaged in reproductive activities had significantly higher DF than all of the other reproductive stages (molting birds had 23.1-170%, and non-reproductive birds 17.8-158% higher DF than other life history stages) (Fig. 28). Courting birds, birds in breeding pairs, and brooders of TIC did not differ significantly in terms of DF, which were all significantly higher than incubators and brooders of TDC (courting birds had 82.5-119%, birds in breeding pairs 58.6-90.5%, and brooders of TIC 76.9-113% higher DF than other life history stages) (Fig. 28). Incubators and brooders of TDC had the lowest DF (Fig. 28).

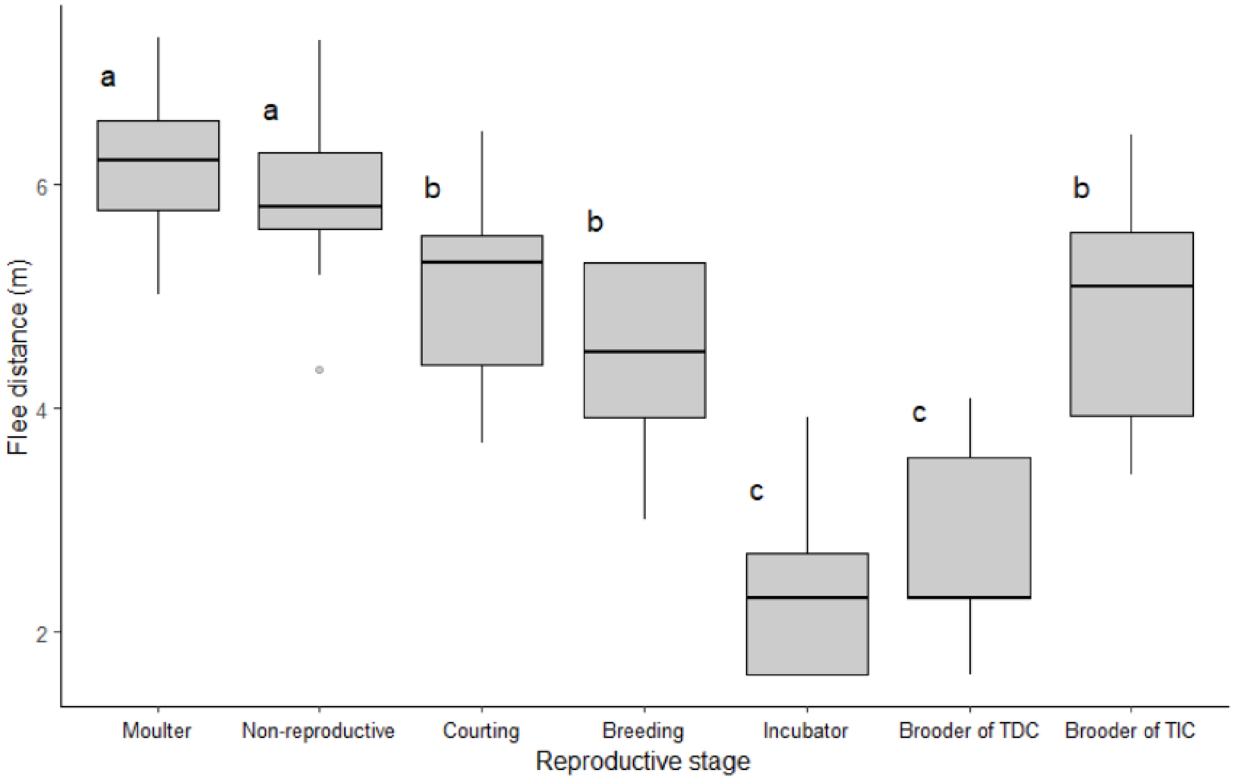


Figure 28. Box and whisker plots of non-zero Distances Fled (DFs) observed across different life history stages in the king penguin (*Aptenodytes patagonicus*) (N=201). Significant differences between groups were determined using Tukey HSD and are distinguished using the letters a,b,c. The horizontal bar represents the median, shading represents the interquartile range, and the vertical line represents the 95% confidence interval.

Not all life history stages (N = 442) behaved aggressively towards the experimenter when approached. Molting birds were never aggressive, birds not in engaged in reproductive activities were aggressive in 4% of approaches (1/24), 5% of courting birds (1/20), and 18% in brooders of TIC (9/50). In contrast, birds incubating or brooders of TDC were aggressive and territorial during most of the approaches. Aggression occurred in 81% of approaches for incubators (203/252), and 80% of approaches in brooders of TDC (62/78). Focusing on groups for which more than one aggressive event was recorded (required for model convergence), differences across life history stage were significant (GLMM, X^2 = 54.8, P<0.001, N = 368). Incubators and brooders of TDC emitted significantly higher aggression than brooders of TIC (incubators compared to brooders of TIC: Tukey HSD, Z = 7.30, P<0.001; brooders of TDC compared to brooders of TIC: Tukey HSD, Z = 6.20, P<0.001). Incubating birds and brooders of TDC were not significantly different from each other (Tukey HSD, Z = 0.09, P = 0.995).

Comparing early and late incubating breeders

Controlling for approach speed prior to AD (LMM, estimate ± SE = 1.00 ± 0.28, $F_{1,94.4}$ = 0.12.9, P<0.001, N = 98), AD was not significantly different between early and late breeders (LMM, $F_{1,95.0}$ = 0.19, P = 0.663, N = 98). Early breeders alerted at 6.61 ± 0.23 m (range = 3.72 – 11.2 m) on average, whereas late breeders alerted at 7.01 ± 0.24 m (range = 2.61 – 9.98 m) on average.

Controlling for approach speed between AD and FID (GLM, estimate ± SE = -1.08 ± 0.43, X^2=7.12, P = 0.008, N = 98), late breeding birds were significantly more likely to flee upon the approach of an experimenter (GLM, X^2 = 5.85, P = 0.016, N = 98). In total, 52% (26/50) of late breeders fled when approached, whereas in comparison, only 44% (22/50) of early breeders fled when approached.

Controlling for approach speed between AD and FID (LM, estimate ± SE = 0.50 ± 0.13, $F_{1,98}$ = 33.2, P<0.001, N = 44), FID was not significantly different between early and late breeders (LM, $F_{1,44}$ = 0.03, P = 0.861, N = 44). Early breeders initiated flight at an average of 2.05 ± 0.40 m (range = 0.67 – 8.46 m), and late breeders alerted at an average of 2.62 ± 0.25 m (range = 1.01 – 6.76 m).

We also found no significant difference in DF between early and late breeders (LM, $F_{1,36}$ = 0.40, P = 0.533, N = 36), after controlling for the significant effect of time of day (LM, estimate ± SE = 0.23 ± 0.11, $F_{1,36}$ = 4.79, P = 0.035, N = 36). Early breeders fled 0.11 ± 0.02 m (range = 0.05 – 0.30 m) on average, and late breeders fled 0.14 ± 0.03 m (range = 0.05 – 0.50 m) on average.

Early and late breeders were equally aggressive to the approaching experimenter (GLMM, X^2 = 0.12, P = 0.730, N = 98). Early breeders emitted aggression towards the approached experimenter in 84% of the approaches (32/50), as did 86% (33/50) of late breeders.

Are fleeing and aggressive behaviors mutually exclusive traits?

When approached by an experimenter, weighted aggression was on average 0.47 ± 1.56 aggressive events (range = 0.00 – 10.4). Individuals that decided not to flee from an approaching observer were also those that were more aggressive towards the observer during approach (incubators and brooders of TDC only, N = 418, $F_{1,415.0}$ = 30.9, P<0.001) (Fig. 29). There was no difference between reproductive status in terms of overall weighted aggression ($F_{1,395.0}$ = 1.42, P = 0.234).

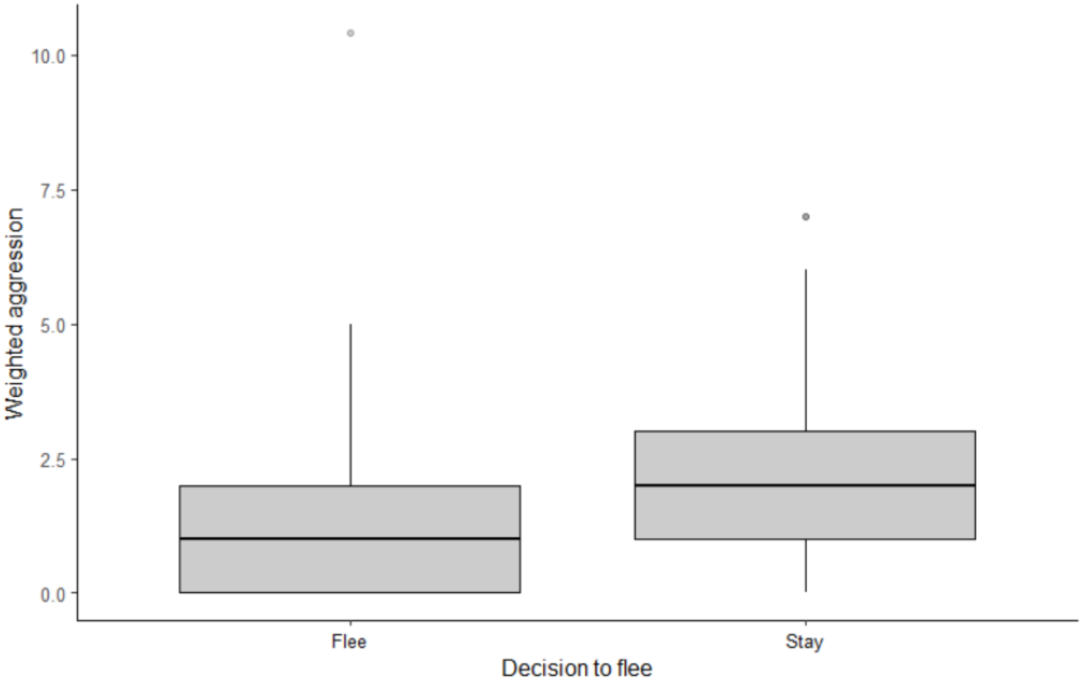


Figure 29. Box and whisker plots of weighted aggression counts displayed by king penguins (*Aptenodytes patagonicus*) towards the approaching experimenter depending on whether they decided to flee or stay. (N=418). All birds sampled were either incubators or brooders of young, thermo-dependent chicks. The horizontal bar represents the median, shading represents the interquartile range, and the vertical line represents the 95% confidence interval.

DISCUSSION

In this study, we used non-lethal human approaches to mimic predation threat and test how antipredator behaviors varied across a range of life history stages in king penguins, some of which were committed to reproduction (courting birds, birds in breeding pairs, incubating birds, and chick-rearing birds) and others not (molting birds, and non-breeders). We found that birds are increasingly less likely to initiate flight and flee shorter distances as they commence and increase their investment into reproduction, from non-reproductive stages to courting and brooding small, thermo-dependent chicks, before becoming flightier after their offspring gain thermo-independence and freedom of movement. Our results also show that birds that initiate breeding later in the season were more likely to flee from approaching threats than early breeders.

Comparing antipredator behaviors across life history stages

We found that life history stage significantly affected bird antipredator behavior including AD, FID, the decision to flee or not, DF, and the probability to emit aggression towards the approaching threat. This would be expected if the different life history stages varied in their costs and benefits of flight (Ydenberg and Dill 1986; Cooper and Frederick 2007). Molting birds and birds not actively engaged in reproductive activities had the longest DF, and the longest FID with courting birds. They also systematically initiated flight upon approach and displayed no aggressive behavior towards the experimenter. Birds in these life history stages had the highest fitness benefit/cost ratio of flight, as they were not defending a territory or courting potential mates, and so there was no trade-off between reproduction and individual survival. In contrast, birds with intermediate FID were courting birds, birds in breeding pairs just settled onto their territory, and brooders of TIC, and birds with intermediate DF were courting birds, birds in breeding pairs just settled onto their territory, and brooders of TIC. Most of these approaches ended up in the bird fleeing non-aggressively, with the noteworthy exception of brooders of TIC (6% did not flee and 18% were aggressive towards the approaching experimenter). Finally, birds in breeding pairs just settled onto their territory and incubating birds had the lowest FID, while incubating birds and brooders of TDC had the lowest DF. For these categories, the fitness benefit/cost ratio is lower, since birds face a trade-off between the fitness gains from reproduction vs. the fitness costs suffered from potential injury or death. For instance, by initiating flight, courting birds risk losing the energy they have invested into courting a partner, birds in breeding pairs settled onto their territory risk losing their partner or breeding territory, while incubating birds and brooding birds risk losing their egg/young chick. It is important to note that for incubating birds and brooders of TDC, distances fled (DFs) were substantially shorter than for other life history stages. This is because incubating birds and brooders of TDC necessarily flee with the egg/young chick on top of their feet, restricting their movement. The most they can do without completely abandoning the offspring is to waddle a couple of meters and cluster with neighboring conspecifics within the colony, benefitting from predation dilution, confusion, mobbing, and selfish herd effects (Hamilton 1971; Cresswell 1994; Boland 2003; Dias 2006; Quinn and Cresswell 2006; Graw and Manser 2007; Olson et al. 2013). In contrast, other life history stages not constrained in their movements by an egg/chick/aggressive neighbors, were able to flee over greater distances (4-8 m). It is clear that incubators and brooders of TDC face the strongest fitness trade-off, as they could potentially abandon reproduction altogether and flee over greater distances; however, this strategy was never found to occur. Two, non-mutually exclusive, explanation might explain this result. First, the actual fitness benefits of fleeing from predation in a king penguin colony are lower than the fitness benefits of clustering with other conspecifics. An isolated adult may indeed be at more risk of being predated than if it clusters with aggressive neighbors (Côté 2000), mobbing and overwhelming the predator. Second, the fitness costs of abandoning reproduction are extremely high in this species. King penguins are long-lived seabirds, and therefore fitness is expected to depend more on adult survival than the current breeding attempt (Lack 1947, 1948; Roff 1992; Stearns 1992), i.e., adults should favor their own survival as they will have chances to breed in subsequent years. However, in this species, the energy commitment to reproduction is extremely high

(Cherel et al. 1988; Groscolas et al. 2000, 2008; Groscolas and Robin 2001), and reproduction only occurs every second to third year depending on when the current reproduction event is failed (Weimerskirch et al. 1992; Van Heezik et al. 1994; Olsson 1996).

Without parental care, eggs and thermally dependent king penguin chicks are highly vulnerable to predation (Hunter 1991; Descamps et al. 2005). Accordingly, incubators and brooders of TDC were also the only life history stages that did not flee in approximately half the approaches. Rather, these birds adopted an aggressive stance towards the approaching experimenter, defending their egg/young chick and territory position, rather than attempting to flee. Similar results were found in Magellanic penguins (*Spheniscus magellanicus*), which were least likely to flee, have shorter FID, and emit the most threat behaviors during incubation than during settlement and molt (Villanueva et al. 2014), and in Adélie penguins (*Pygoscelis adeliae*), where commuting birds had the higher FID than brooding birds (Wilson et al. 1991).

AD was higher in molting birds and birds not actively engaged in reproductive activities than in all other reproductive stages (courting birds, birds in breeding pairs just settled onto their territory, incubating birds, and brooding birds). This result is somewhat surprising given that studies generally show that animals increase vigilance behavior when breeding. For example, reproductive females with accompanying offspring often display increased vigilance behavior (e.g., in a range of African mammals, Burger and Gochfeld 1994; elk, *Cervus elaphus*, Childress and Lung 2003; and eastern grey kangaroo, *Macropus giganteus*, Carter et al. 2009). Similarly, incubating Magellanic penguins show higher AD than molting and settling birds (Villanueva et al. 2014). One explanation may be the investment into egg/chick care in breeding birds is done at the detriment of time spent in vigilance behaviors, explaining shorter AD. Alternatively, birds that are molting or not actively engaged in reproductive activities typically form mobile groups on the outskirts of the breeding colony. In addition to the well-known benefit of risk dilution (Dehn 1990; Cresswell 1994; Boland 2003), this dynamic social environment is likely to transmit information on predator presence to the surrounding neighbors rapidly (many-eyes hypothesis (Pulliam 1973; Lima and Dill 1990; Burger and Gochfeld 1991; Mayer et al. 2019), since predators entering a grouping of molting or non-breeding penguins will create a movement ripple travelling through the group (TLH, PB, JPR, BG, VAV; personal observations).

We have previously found that higher conspecific densities may also distract incubating penguins from antipredator behaviors (Hammer, Bize, Gineste, Robin, Groscolas, Viblanc, 2022, submitted). The distracted prey hypothesis (Chan et al. 2010; Petrelli et al. 2017) proposes that the processing of social cues and interactions with conspecifics may interfere with predator vigilance (Mooring and Hart 1995; Yee et al. 2013). Courting birds involved in the process of mate choice may also be distracted from predator vigilance, while birds in breeding pairs, incubating birds, and brooding birds contend with repeated and frequent territorial aggressions from neighbors (Côté 2000). In contrast, molting birds, and birds not actively engaged in reproductive activities are not territorial, not occupied by acquiring a mate or territory, and may more easily devote a larger part of their time budget to predator vigilance.

Antipredator responses and brood value

Our results show that (1) breeding pairs without an egg and incubating birds had the lowest FID (lower than brooders of TDC and TIC), (2) DF was shorter in incubating birds and brooders of TDC than brooders of TIC, (3) incubating birds and brooders of TDC defended the brood with equal presence of aggression upon approach by the experimenter (~50% not fleeing, and ~80% displaying aggression), and (4) brooders of TIC were less likely to stay and defend their young aggressively against the approaching experimenter (only 6% not fleeing, and 18% displaying defensive aggression). In addition, brooders of TIC fled independently of their chicks, while brooders of TDC always fled with their chick on top of their feet, resulting in much shorter DF. Our results only marginally support the brood value hypothesis, as brooders of TDC did not have lower FID and DF than incubating birds, despite having older offspring which should be of higher brood value (Trivers 1972; Barash 1975; Montgomerie and Weatherhead 1988; Frid and Dill 2002). However, the highest rates of defensive behaviors were observed in stages that had dependent young (eggs/young chicks). In line with the brood value hypothesis, territorial brood defense is known to increase from incubation to young, non-thermally emancipated chick brooding in king penguins (Côté 2000), showing an increase in brood value as the brood ages, yet this increase in brood defense was not reflected in FID and DF.

Our results show that king penguin responses to approaching predators are similar to what would be expected from species with altricial young (Barash 1975). In species with altricial young, investment into offspring defense increases gradually from incubation to brooding, with a peak at the end of the nestling period, then, when the offspring are of an age to independently flee from predators themselves, parental investment in offspring defense sharply decreases (Andersson et al. 1980; Redmond et al. 2009; Strnadová et al. 2018). At the point when offspring are able to mount a measure of self-defense, flee independently, or group/shelter for protection from predators by themselves (e.g. in creches in penguins, Stonehouse 1960; Weimerskirch et al. 1992; Descamps et al. 2002), offspring defense by the parent becomes wasteful and redundant (Koskela et al. 2000; Thünken et al. 2010). Our results are consistent with those found in other penguin species. In Magellanic penguins (Cevasco et al. 2001; Villanueva et al. 2014), incubators and brooders of young chicks have shorter FID, flee less often, and displayed greater aggressive defense behavior than brooders of larger, more mature chicks. In Adélie penguins, birds at nests containing large chicks have longer FID than those at nests containing small chicks (Wilson et al. 1991). In African penguins, *Spheniscus demersus*, parents with young chicks are more aggressing to approaching humans than incubating birds, yet birds with older chicks were the most likely to initiate flight (Pichegru et al. 2016). These same results are also seen in mammals and fish with altricial young, for example, bank voles, *Clethrionomys glareolus* (Koskela et al. 2000), and a cichlid fish, *Pelvicachromis taeniatus* (Thünken et al. 2010).

Mechanistically, changes in parental commitment to offspring have been suggested to be underpinned by parental stress responsiveness to external threats, with attenuated responses of the Sympathetic-Adrenal-Medullary (SAM) and Hypothalamic-Pituitary-Adrenal (HPA) axes occurring when the relative reproductive value of the offspring is high (Lendvai et al. 2007; Lendvai and Chastel 2008; Bókony et al. 2009; Schmid et al. 2013; Viblanc et al. 2015). Studies conducted on king penguins show that hormonal (Viblanc et al. 2016) and heart rate (Viblanc et al. 2015) stress responses to non-lethal human approaches are attenuated in birds brooding young chicks compared to birds incubating an egg, suggesting a redirection of parental physiology geared towards offspring care rather than adult survival. However, these studies have not considered whether such attenuated physiological stress responses are reflected in attenuated parental alert and flight behavior, nor have they considered differences in parental responses to approaching threats when parents were brooding chicks of different ages. Future studies in king penguins should look more closely at stress responses their relationship to antipredator behaviors with a broader focus on different life history and reproductive stages.

Comparing early and late breeders

Birds breeding early vs. late in the season were expected to show different anti-predator responses and varying degrees of investment into offspring defense as the breeding success of early and late breeders differs substantially (Weimerskirch et al. 1992; Van Heezik et al. 1994; Olsson 1996). While AD, FID, DF, and aggression were comparable between early and late breeders, late breeders were significantly more likely to initiate flight when approached than early breeders. According to the brood value hypothesis (Montgomerie and Weatherhead 1988; Redmond et al. 2009), late breeding king penguins should be less prone of defending their brood against potential predators than early breeders since their likelihood of success is virtually null, and these birds have the possibility to breed again in subsequent years. Higher fitness by individuals initiating their reproduction earlier in the season is frequently observed in birds (as well as mammals) (Bednekoff 1996; Kokko 1999; Götmark 2002; Williams et al. 2014; Germain et al. 2015). Accordingly, early breeders were found to defend their brood more than late breeders, for example in red-winged blackbirds *Agelaius phoeniceus* (Biermann and Robertson 1981), house sparrows *Passer domesticus* (Klvaňová et al. 2011), eastern kingbirds *Tyrannus tyrannus* (Redmond et al. 2009), and great tits *Parus major* (Onnebrink and Curio 1991). Late breeding snow petrels (*Pagodroma nivea*) are also more prone to nest abandonment than early breeding birds (Goutte et al. 2011).

Conclusions

We found that antipredator behaviors changed in concert with changes in the cost of flight, in accordance with optimal escape decisions. Non-reproductive birds were more prone to flight, fled further, and were less aggressive in response to an approach by a human experimenter. Reproductive birds, in particular incubating and brooding birds of young chicks were the least prone to flight, and frequently stayed and exhibited aggressive defensive behavior, yet offspring defense reduced as chicks gained independence of movement, in accordance with results seen in species with altricial young. Finally, late breeding birds, who have much lower reproductive success than early breeding birds, were more likely to flee upon approach, suggesting lower perceived brood value. Our results demonstrate that antipredator behavioral responses are dynamic and shaped by the costs of flight and site fidelity, in particular by current reproduction and perceived brood value.

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General Discussion

This thesis has analyzed the antipredator behaviors of king penguins when ashore in their natural colonial environment. Antipredator behaviors were investigated using a standardized, non-lethal approach by a human observer that allowed for the measurement of when an individual became alert (Alert Distance, AD), initiated flight away from the observer (Flight Initiation Distance, FID), the total distance the individual fled from the observer, (Distance Fled, DF), and the total number of aggressions displayed during the approach either towards neighboring conspecifics or towards the approaching observer. Over the first three chapters, this thesis aimed at explaining the variation seen in these antipredator behaviors by exploring to which extent they were individually repeatable (in turn, characterizing individual personalities), and the extent to which they were shaped by habituation, human disturbance, the social environment, life history stage, and residual reproductive value. Below, I will briefly recapitulate the main findings of the thesis before proceeding to a critical assessment of the limitations of the studies presented and future perspective projects that could stem from this thesis.

1. Overview of the project

1.1 Exploring the variability of antipredator behavior in relation to personality and abiotic environmental factors and human disturbance

In understanding the variability of antipredator behavior in colonial king penguins, one of the first questions I addressed was whether individual variations in AD or FID was mostly shaped by abiotic environmental factors or whether inter-individual differences could also be explained by factors intrinsic to individual birds, such as personality. To do this, Chapter 1 assessed whether AD and FID were repeatable in the king penguin, that is, whether some individuals were consistently faster to detect an approaching threat at greater distances than others and/or to flee from the approaching threat, regardless of environmental stochasticity.

The measure of behavioral repeatability is essential to test for the presence of personality traits (Sih et al. 2004b, Réale et al. 2007, Dingemanse and Wright 2020). It is generally assumed in the literature that FID can act as a personality trait (Carter et al. 2010, Evans et al. 2010, Atwell et al. 2012, Highcock and Carter 2014, Young et al. 2015, Arroyo et al. 2017), but I considered that before more work is performed based on that assumption, repeatability should be established in the species. Indeed, FID has been found to be repeatable in previous studies (Carrete and Tella 2010, Carter et al. 2012, Seltmann et al. 2012, Petelle et al. 2013, Møller 2014, van Dongen et al. 2015, Cabrera et al. 2017), but the repeatability of AD has not been previously explored. Accordingly, in Chapter 1, I showed that FID (r=0.26, CI_{95} = [0.010, 0.511]), and the decision to flee (r=0.57, CI_{95} = [0.110, 1.686]), but not AD (r=0.15, CI_{95} = [0, 0.313]), were weakly to moderately repeatable in the king penguin, and thus could most likely be interpreted as personality traits (but see Dingemanse and Wright 2020).

In Chapter 1, I also tested whether king penguins habituate or sensitize to repeated approaches, and whether antipredator behaviors vary between two colonies with differing exposure to human disturbance. This allowed testing the extent to which variation in the environment affected antipredator responses of individual birds. It is not uncommon for animals to habituate rapidly to benign approaches by human approachers (Burger and Gochfeld 1981, 1990, Fernández-Juricic et al. 2002, Carter et al. 2012, Petelle et al. 2013, Bateman and Fleming 2017, Cabrera et al. 2017, Uchida et al. 2019), and I expected the colony with more human disturbance to be habituated to human presence. However, I did not find clear evidence for behavioral habituation to repeated approaches, and nor did I find a difference in responsiveness between the two colonies. In this study, I also attempted to quantify some of the variation seen in AD and FID. I found that weather conditions at the time of approach could affect both AD and FID. In warm, sunny weather, AD increased, while in rainy, windy weather, birds were more likely to flee but waited longer before initiating flight. It is apparent that weather is an important factor to control for when measuring AD and FID. I also tested for speed of approach and found that faster approach speeds lead to longer FID, a result commonly found across studies (Cooper 1997, 2003b, 2006, Burger 1998, Cooper et al. 2003, 2009a, 2009b, Stankowich and Blumstein 2005, Stankowich and Coss 2006, Cooper and Whiting 2007, Bateman and Fleming 2011b, Samia et al. 2016). One probable explanation resides in the notion that faster speed of approaching predators signals intent and increases the apparent threat of the approach (Frid and Dill 2002, Stankowich and Blumstein 2005). By controlling for speed of approach in all later chapters, I discovered that speed of approach reliably influences FID, and sometimes – but not always - AD, and needs to be accounted for in all analyses.

Overall in the first chapter of my thesis, I demonstrated that in breeding king penguins, FID and the decision to flee are repeatable, but not AD, and that king penguins did not show habituation or sensitization in terms of their behavioral response to human approaches. AD and FID were influenced by environmental conditions such as the weather, and faster speeds of approach led to longer FIDs.

1.2 Exploring the effects of colonial group living on antipredator behavior

Once I had established the extent to which antipredator behaviors in breeding king penguins were influenced by intrinsic characteristics of the birds, and defined the potential confounding environments factors (e.g., weather) to account for when analyzing AD and FID, I proceeded to explore how the highly aggressive colonial environment of breeding king penguins affected antipredator behaviors.

Group living is thought to have evolved because of the many important antipredator fitness benefits it provides, owing to the mechanisms of shared vigilance ("many-eyes" hypothesis) (Pulliam 1973, Caraco et al. 1980, Lima 1995), risk dilution ("dilution effect" hypothesis) (Inman and Krebs 1987, Dehn 1990), and increased relative safety in the center of the group ("selfish herd" hypothesis) (Hamilton 1971). However, aggregating into dense social groups also carries costs, since external social stimuli, such as conspecific aggression, may distract individuals from anti-predator behavior ("distracted prey" hypothesis) (Chan et al. 2010). Hence, in Chapter 2, I tested for the effects of the social environment on antipredator behaviors, as this may be an important source of variation affecting AD and FID in colonial seabirds. Specifically, I tested: the "many-eyes", "dilution effect", "selfish herd", and the "distracted prey" hypotheses. I found that birds engaged in aggressive interactions with neighbors were less likely to flee, and that increasing relative local neighbor density at low and medium overall colony density resulted in a decrease in bird AD, both results supporting the "distracted prey" hypothesis. However, at maximal overall colony density, increasing relative local neighbor density resulted in longer AD, supporting the "many-eyes" hypothesis. These contrasting results are especially interesting as they suggest that neighbors can both provide benefits and generate costs with regards to predation.

On one hand, at low and medium colony densities, neighbors distract from predator detection, possibly due to social monitoring and aggressive interactions. Colonial king penguins are highly aggressive and territorial during reproduction (Côté 2000, Viera et al. 2011), and previous studies have shown how social aggression and high social densities could be a potential source of stress in these seabirds (Viblanc et al. 2012b, 2014a, 2014b). It is clear that king penguins are highly sensitive to the behaviors of their neighbors, even in instances when they are only bystanders to the social interaction in question (Viblanc et al. 2012b). Such social monitoring is likely necessary to ensure that breeding territories are secured and the egg/chick protected, especially as offspring age and reproductive investment increases (see Côté 2000 and see Chapter 3). However, this apparently comes at a cost in terms of antipredator detection, with potential detrimental consequences on fitness. On the other hand, at high colony densities, having more neighbors also means that more individuals are present to detect an approaching threat and alert surrounding birds, thus leading to increased detection and earlier ADs. I found no support for the "dilution effect" or the "selfish herd" hypotheses in this study.

1.3 Exploring the effects life history stage and residual reproductive value on antipredator behaviors

Having considered how group-living might affect antipredator behavioral decisions in breeding king penguins, I turned to understanding how behavioral decision were shaped by the investment into reproduction (Trivers 1972, Montgomerie and Weatherhead 1988, Clark and Ydenberg 1990a, 1990b, Lima 2009, Dowling and Bonier 2018), a fundamental trade-off in life history theory. For breeding adults, the decision to stay and protect their young against a predator, potentially risking serious injuries or death, or to flee and abandon reproduction altogether, is conditioned by a trade-off between the value of current reproduction vs. that of future breeding opportunities (Williams 1966, Trivers 1972, Montgomerie and Weatherhead 1988). Thus, in Chapter 3, I explored variation in AD, FID, and DF, by comparing across life history stage. I found large and significant different in FID and DF between the life history stages, and also increased AD in non-reproductive stages. The different life history stages have different fitness costs associated with initiating flight and different degrees of site fidelity, and it is reflected in the FIDs and DFs. Birds with low fitness costs of flight and low site fidelity (i.e., molting birds non-reproductive birds which do not have offspring to lose) had the longest FIDs and DFs. Birds courting or in breeding pairs just settled onto a territory, and brooders of larger thermally independent chicks had intermediate FIDs and DFs, because their fitness costs of flight increased. For these animals, if flight is initiated, they risk losing mates, territory, or offspring. The shortest FIDs and DFs were seen in incubating birds and brooders of young thermally dependent chicks. It is important to observe that these animals incubate/brood the egg/young chick on top of their feet, drastically reducing the mobility of the adult. This group has the highest costs of flight, as initiating full flight would necessitate abandoning the egg or young chick to predation, in other words, fully abandoning reproduction.

In this chapter I also tested the brood-value hypothesis and parental investment. Parental commitment to offspring is expected to increase, and FID decrease, as the relative reproductive value of the offspring increases (the “brood value hypothesis”) (de Jong et al. 2013, Arroyo et al. 2017), and if the odds of offspring surviving to sexual maturity are high (Trivers 1972). As offspring age, their likelihood of survival to independence increases, leading to higher offspring value (Barash 1975, Andersson et al. 1980, Ackerman and Eadie 2003, Redmond et al. 2009, Svagelj et al. 2012). Accordingly, I expected FIDs to decrease, and nest defense increase as offspring aged, up until a critical point when the offspring gains the ability to independently defend themselves against predatory attacks (Barash 1975, Andersson et al. 1980). The timing of offspring independence depends on whether the offspring is born/hatched altricial or precocial. Precocial offspring are able to mount antipredator defenses shortly after birth/hatching and so rely less on parental care shortly after, while altricial young continue to rely on parental care for some time (Barash 1975, Andersson et al. 1980). In our study, incubators and brooders of young chicks had the shortest FIDs and DFs, showing high investment in offspring defense. These life history stages also displayed the highest levels of aggression towards the approacher and regularly chose to stay and aggressively defend their offspring rather than initiating flight. None of these birds (incubators and brooders of young chicks) abandoned their offspring, instead choosing to flee with the offspring resting on top of the parent's feet. However, support for the brood value hypothesis was low, as brooders of young chicks did not have shorter FID/DF than incubating birds despite having offspring of older age. When the chicks were older, thermally independent, and had independence of motion, parental investment into offspring defense sharply decreased and parental FIDs and DFs increased again. At this stage, the offspring are able to independently flee from predators and parental investment in offspring defense becomes redundant, hence the reduction in parental investment at this stage. These results confirm what is expected from species with altricial young (Andersson et al. 1980, Wilson et al. 1991, Pavel 2006, Pichegru et al. 2016)

Finally, in this chapter, I also explored variation in antipredator behavior between early and late breeding birds. Substantial differences exist in reproductive success between early and late breeding birds in the king penguin: late breeding birds have very little chance of successfully fledging a chick when compared to early breeding birds (Weimerskirch et al. 1992, Van Heezik et al. 1994, Olsson 1996, Stier et al. 2014). Due to this, parental investment into offspring defense from predators should be greatly reduced in late breeding king penguins. I found that late breeders were more likely to initiate flight when approached by a human experimenter than early breeding birds, suggesting late breeding birds have reduced reproductive investment in their brood.

General conclusions

Across all the studies, I found that AD, FID, and DF were easy behaviors to observe and record in the king penguin. FID, in particular was found to be repeatable and act as a personality trait in agreement with the literature, where FID is commonly used as a measurement of boldness, one of the five main aspects of personality (Réale et al. 2007). FID is interesting to study, as not only is it linked to various factors (e.g., apparent risk in the approach, residual reproductive value), but as a personality, it can also be explored in terms of bold/shy individuals and individual quality, and therefore test whether individual life history strategy leads to differential selection and fitness advantages. AD, on the other hand, has been shown in the literature to be more complicated to measure than FID (Blumstein 2010), although in the king penguins the moment of alert is a fairly conspicuous behavior. AD, unlike FID, was not found to be a personality trait and tended to be more context dependent than FID. AD was affected by disturbances in the environment (such as the weather or social distractions).

2. Effects of the environment on antipredator behaviors

2.1 Weather conditions

In Chapter 1, weather was found to influence both AD, FID, and the decision to initiate flight. In warm, windy, sunny weather, AD decreased, while in windy, rainy weather, birds were more likely to flee but waited longer before initiating flight. According to a meta-analysis by Cherry and Barton (2017) windy weather has been dependently demonstrated to have a negative effect on predator detection, consistent with what I found in the king penguin with shorter AD in sunny, windy weather. Weather has also been found to have an effect on FID, particularly temperature in animals that are sensitive to temperature (Rand 1964, Bulova 1994, Samia et al. 2016), such as ectotherms and incubating birds. In ground nesting birds (five Charadriidae and three Camprimulgidae), flight initiation distance was shorter during mid-day, showing reduced tendency to abandon the eggs when the temperature was unfavorable for prolonged exposure, suggesting escape behavior was mediated by thermal regulation (Wilson-Aggarwal et al. 2016). The king penguins in this study may have delayed FID in windy, rainy weather, in order to limit the risk of egg exposure to unfavorable weather conditions (eggs may lost up to 0.19°C per minute if left unattended, Groscolas et al. 2000), or because the conditions made it hard for them to detect approaching predators. Teasing apart these possibilities may prove complicated.

From consistently testing for weather in the different chapters of this thesis, we found that weather, while it may affect AD and FID, did not always do so dependably or in the same strength and direction depending on the study. While we found effects of weather on AD and FID in Chapter 1, which measured behaviors over a period of 3 days, we did not detect any effects of weather in Chapter 2 and 3 where measurements of antipredator behaviors were recorded over periods of at least several months. It appears that weather while weather impacts AD and FID at the moment of approach, weather does not have as strong an impact or explain as much variation in AD and FID as other factors, such as the social environment or life history status changes of the individual. Regardless, given that weather variables appear to absorb part of the variance in behavioral measures, it remains important to continue to control for it in future analyses, since this is likely to provide more meaningful effect sizes for other variables of interest. Besides, one should keep in mind that the effects of weather may be inconsistent and hard to interpret, suggesting that the effects of weather variables on antipredator behaviors depends on the study and data set analyzed, as well as the type of analyses and factors considered in the analyses. Further studies are needed to elucidate the relationships between weather and antipredator behaviors. An example of such a study would be to measure the same life history stage over multiple years to test for differential yearly effects of weather. Alternatively, birds could be repeatedly approached over 6+ days within the same season, which would also better test antipredator behaviors from a personality vs. habituation/sensitization perspective.

2.2 Social groupings

In Chapter 2, we tested how group living impacts antipredator behaviors in colonially breeding king penguins. We found that at low and medium colony densities, increasing numbers of neighbors lowers AD, possibly due to increased social monitoring and aggressive interactions. Yet, at high colony densities, increasing the number of neighbors increased AD, supporting the "many-eyes" hypothesis (Pulliam 1973, Caraco et al. 1980, Lima 1995). In this study we did not find support for the "risk dilution" (Inman and Krebs 1987, Dehn 1990)or "selfish herd" (Hamilton 1971) hypotheses. Yet, this does not necessarily mean that king penguins do not benefit from risk dilution or location within the colony. It is possibly that our study did not test in such a way as to bring these beneficial effects to light. For instance, there must be a benefit of risk dilution since these colonies are in the tens of thousands of individuals (Delord et al. 2004, Barbraud et al. 2020) and only a few individuals can be taken by predation at any point in time (but see discussion below). On the occasion when a breeder chose an isolated breeding territory, predation of the egg rapidly followed (personal observation). Less dense areas of the colony also seemed to suffer from increased offspring predation (personal observation). Further, it is rare to observe birds alone as they consistently tend to form groupings, even molting and non-reproductive birds cluster into groups. Comparing one part of the colony to another part of the colony may not create enough variation to compare the relative effects of risk dilution, as the benefits of risk dilution may reach a maximum at larger group sizes (i.e., diminishing returns, Dehn 1990). Perhaps a better designed study would be to compare individuals alone or in small groups to individuals in much larger groups and avoid studying the main breeding colony. Another option would be to manipulate social density within the colony. This could be done using exclosure pens to artificially reduce breeding density around focal birds and then recording bird behavior and potential predation pressure. However, it does also raise the question of experimentally inducing a potential situation where the risk on the bird(s) and its reproduction is increased.

There is also evidence that the selfish herd effect may play a role in king penguin colonies. In king penguins, peripheral birds in the colony have greatly reduced reproductive success, possibly because peripheral breeding birds have about twice as many interactions with predators than central birds (Côté 2000, Descamps et al. 2005). Peripheral positions in the colony also tend to be occupied by late breeding birds, which may contribute in explaining the lower reproductive success rate of late breeding birds in this species (Côté 2000). This strongly implies that central positions in the colony are of higher quality due to reduced predation risk, and indeed central positions tend to be occupied by the most aggressive birds (Viera et al. 2011). Corticosterone has been found to be elevated in areas of higher density (Viblanc et al. 2014a), possibly due to increased social stress and aggression in central positions, yet it is unclear whether this is correlation or causation. Central birds may also benefit from increased predator detection, as when a predator (or human observer) approaches from the periphery of the colony, ripples of disturbance follow the approach, creating much noise and aggressions and alerting surrounding birds (personal observation). Although I did an analysis in Chapter 2 that compared AD and FID across a range of ranks, sample collection was not distributed evenly at high ranks (see discussion below), and so I propose that this study should be conducted again with some modifications. A simple study could measure the AD and FID of central and peripheral birds instead of a range of ranks, particularly looking at birds of high rank (rank = 10+), compared to those on the periphery (ranks = 1-2).

The high level of territorial aggression seen in breeding king penguins may provide more benefits than just protecting territory against conspecifics. This network of aggression also makes it difficult for any predator to infiltrate densely packed areas of the colony without risking sustaining injury. This is perhaps why peripheral territories suffer higher rates of predation (Côté 2000, Descamps et al. 2005), as they lack sufficient numbers of neighbors to succesffully attack/mob incoming predators. When a breeding king penguin is targeted by a predator, they shuffle away with their egg/chick on top of their feet until they are blocked by nearby neighbors aggressively defending their territory (personal observation). The ensuing aggression implicates everyone (neighbor and predator alike), but the result is that it is much more difficult for successful predation to occur. It is worth wondering why this extreme aggression evolved in king penguins; is it perhaps a byproduct of defense against predators, or is it just extreme territorial defense that has the positive side effect of also alleviating predation? Studying bird behavioral responses to human approaches in two different colonies that vary in terms of predation pressure on land would be of interest to test if breeders are more spaced out and less aggressive towards each other when predation pressure is lower.

2.2.a Critical evaluation and perspectives

Colony living in the king penguin likely provides antipredator benefits that helps reduce predation on susceptible life history stages: eggs and chicks. This study shows clear evidence that group-living leads to antipredator benefits in the form of increased predator detection at high colony density, although the actual fitness benefits remain to be thoroughly tested. There are other reasons for forming colonies, one of which being limited space (Danchin and Wagner 1997), yet, despite there being other available beaches where king penguins could potentially settle, they do not utilize these beaches and instead continue to group in the large colonies. Colonies may also form for the benefit of transmitting information such as the location of good forage spots (Boulinier et al. 1996, 2008), yet it is unclear whether king penguins do this.

While it is likely that king penguin colonies benefit from risk dilution and selfish herd effects, our study was not able to pick up on these effects. I think that comparing different sections of the colony possibly masked the benefits of risk dilution as they may already have been maximal in a group of that size. Comparing groups of more varying sizes, perhaps utilizing smaller groups that form on the periphery of the colony, may provide more power in future studies to detect such effects. In Chapter 2, while we included rank as a predictor to explain the selfish herd hypothesis, birds were easier to approach and sample when overall colony density was low. This resulted in birds being approached further into the colony (higher rank) when density was low, but when density was high, sampled birds were more numerous on the outskirts of the colony (lower ranks) to avoid disturbing the breeding colony too much. Although I found no collinearity issue (VIF = 1.33) in the analyses, in retrospect, it would have been better to sample ranks evenly – though the question would then be about our impact on colony breeding and disturbance. For similar reasons, the number of birds in each area were not evenly sampled (depending on accessibility and ease of sampling). Even sampling would allow further comparisons of variations between colony locations, known to differ in their exposure to various factors, including human disturbance (Viblanc et al. 2012a), and predators (Côté 2000)

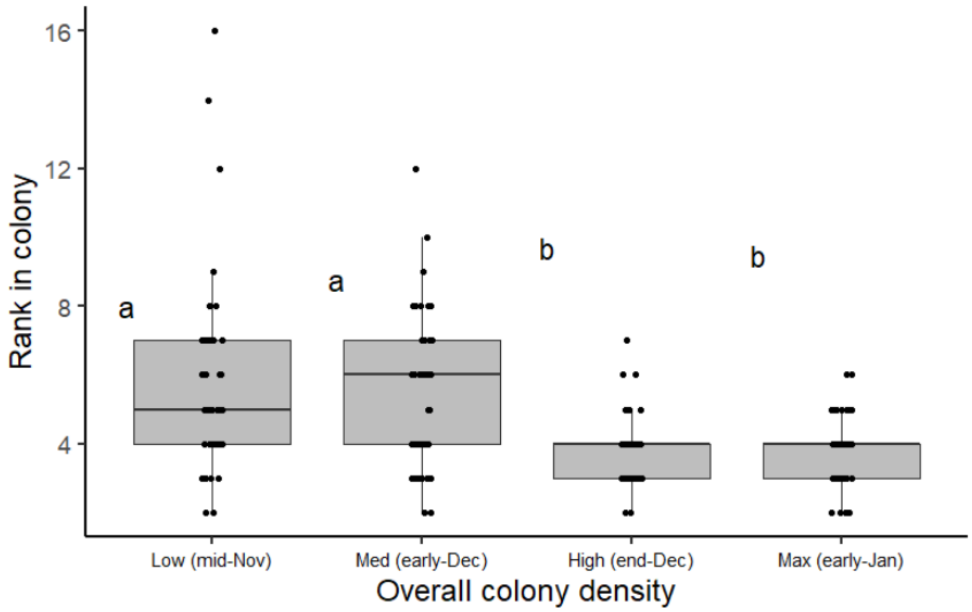

Figure 30. Ranks of the birds measured in Chapter 2 versus overall colony density. Higher ranks were not measured as commonly at higher colony densities. a, b, indicate significant differences.

Finally, the argument could be raised that instead of seeing the effects of the colony getting denser over time, we are instead seeing the effects of later and later breeding. This is the reason for which I studied birds of similar breeding status when the colony was of low, medium, high, and maximal density and, in my analyses centered local density around each colony density in order to separate the effects between local density and overall colony density. In other words, the question I asked was: regardless of timing, for a mean density in the colony – how much did the local environment of an individual bird vary above or below mean density, and how much did this affect bird behavioral responses to our approaches. Doing so limited the potential bias due to the advancing breeding season, since the effects were made statistically independent. Nonetheless, building upon this correlative approach, we now need an experimental approach where local densities of neighbors are actually increased or decreased (e.g. using exclosure pens) to more accurately tease apart the effects of colony density and breeding timings.

2.3 Reproductive status and life history stage

In Chapter 3, we found that life history stages that were molting or not involved in reproductive activities had the highest AD, FID, DF, and the lowest rates of aggression towards the experimenter. Courting birds, pairs just settled into their breeding territory, and brooders of large chicks had intermediate FID, and DF, while incubators and brooders of young chicks had the shortest FID and DF.

Differing fitness costs of flight and site fidelity play a large role in determining antipredator behavior. When the fitness cost of flight is higher (for example when offspring are present), flight behaviors are strongly reduced. Meanwhile, animals with low fitness costs of flight and low site fidelity will flee readily. Furthermore, I found parental investment in antipredator defense lowered when the chick was emancipated and able to flee predators on its own (as is seen in altricial species, Andersson et al. 1980; Wilson et al. 1991; Pavel 2006; Pichegru et al. 2016). Parental investment in offspring was, in general, high. Parents frequently chose to stay (47% of incubators and 53% of brooders of young chicks) and instead stayed and defended their offspring aggressively. When flight was initiated, it was always with the egg/young chick on top of the feet. No parents abandoned their offspring in this study. This raises the question of parent-offspring conflict: when does it become less advantageous to defend your offspring than yourself? Apparently, for king penguins, defense of current offspring is of high value relative to future reproduction, which is surprising given that they are long-lived birds which should favor individual survival over current reproduction.

There remains much to be studied in terms of brood value. A more detailed experiment could be performed that follows AD, FID, DF, and antipredator aggression weekly as offspring age up until shortly after thermal independence. This would give a clearer idea of the trends that my study noted. It would also be interesting to link the progression in antipredator behaviors to changes in hormonal levels (mainly corticosterone and prolactin) and stress responses. It is known in king penguins that corticosterone and heart rate responses increase when the eggs hatch: brooders have 55% higher corticosterone levels than incubators (Viblanc et al. 2014a), and corticosterone stress responses are markedly attenuated in brooding birds compared to incubating birds (Viblanc et al. 2016), as are heart rate increases in response to a stressor (Viblanc et al. 2015). Prolactin, meanwhile has been found in emperor penguins (*Aptenodytes forsteri*) to increase around the time of egg laying and continue to be secreted at high levels throughout incubation and brooding (Lormée et al. 1999), and is thought to be involved in the maintenance of parental care in birds (Angelier et al. 2016). Declines in prolactin have been associated with the cessation of parental care (Boos et al. 2007). In king penguins, prolactin has been found to reach high plasma concentrations in incubating birds and remain high throughout the fledgling period (Cherel et al. 1994b), and are depressed when parents abandon reproduction (Groscolas et al. 2008). These hormones and stress responses may shape antipredator responses in breeding animals. A future study could measure the changes in FID throughout the breeding cycle and immediately sample prolactin and corticosterone, however these samples must be performed within 5 minutes of the initial disturbance as corticosterone levels increase due to hormonal stress response to human approach (Viblanc et al. 2016).

During reproduction, adults take it in shifts to incubate/brood the egg/chick while their partner goes to sea to forage. It is currently unknown how antipredator behaviors vary within shifts. A shift lasts some 7-14 days, but may last up to around 21 days without complications (Weimerskirch et al. 1992). As a shift lasts a considerable amount of time, with no chance to forage or drink water, energy reserves and therefore body condition deteriorate as the shift progresses. Individuals in poor body condition may have enhanced stress and FID responses (Seltmann et al. 2012, Moiron et al. 2019). In this thesis, the timing during a breeding shift, the age and body condition of the attending bird was unknown. As a long-lived species, it is likely that breeding experience plays a role in antipredator behaviors in king penguins. Are chicks defended more strongly as the parent ages, as each reproductive attempt nears being the last (terminal investment, Angelier et al. 2016)? Do young parents flee more often than older parents, as they still have plenty of opportunities to breed? Long-term studies are needed where the age of the parent is known in order to study changes in AD and FID and explore the effects of current reproduction vs. future reproduction and the influences of terminal investment.

2.3.a Critical evaluation

Chapter 3 was an accumulation of different experiments into one cohesive larger study. Because of this, sample size for each life history stage varied widely. For instance, only 17 birds in a breeding pair were sampled, yet over 250 incubating birds were sampled. Initially, the breeding pairs were only sampled as part of a pilot study, and so the methodology changed slightly between it and later studies. For instance, for some of the earlier studies (courting birds, birds in breeding pairs just settled onto a breeding territory), start distances were not yet standardized at 18 m, hence the variation seen in starting distances in this chapter. Courting birds also had variable start distances: the purpose here originally was to test the effect of start distance on AD and FID, an aspect that was dropped from the final study. Distances Fled were not sampled for all groups (missing from birds in breeding pairs, some incubators, and some brooders of young thermo-dependent chicks). In an ideal world, sample sizes across the life history stages would be even and approach protocols more consistent, bearing in mind that approach protocols were adjusted throughout the year depending on feasibility in the field, preliminary results, and according to other studies conducted in parallel. Density was also not controlled for in this study, which may initially seem like a problem as this was shown to be important for AD in Chapter 2; however, density is expected to vary naturally with life history stage as they are found at different times of the year and in different locations of the colony.

2.4 The consequences of human disturbance

It is worth considering whether humans truly act as predation-free predators in the king penguin and in other species more generally. It is immediately apparent that human approaches result in generalized antipredator responses in the king penguin through AD, FID, DF, and in some cases, aggression. But do they result in a disturbance that diverts time and energy from other fitness enhancing activities such as foraging, parental care, or territorial defense (Frid and Dill 2002, Beale and Monaghan 2004b)? A disturbance is defined as any situation in which an animal behaves differently from its preferred behavior (Boere 1975, cited by Blanc et al. 2006). This includes both natural disturbances, such as a predation attempt or social interaction, and non-natural events, such as those caused by human interactions with wildlife. So far, we have largely discussed disturbance in the form of an approaching predator or threat; however, human activities can have a large impact on animal behavior, as was briefly discussed above in regards to hunting. Human disturbance can take on many forms, and even something as simple as quiet observation may have an impact. Human disturbance has been separated into five main groups (modified from Bateman and Fleming 2017):

1. Ecotourism: responsible visitation to a natural area that conserves the environment, sustains the well-being of local people, and involved education. This includes animal observation and watching
2. Wildlife tourism: recreational engagement with wildlife where the focal organism is not removed or permanently affected
3. Natural area tourism: incidental interactions with wildlife due to the action of other tourist activities. This includes hiking, skiing, biking, snow-mobiles, etc
4. Consumptive wildlife tourism: recreation in which the animal is harmed or harvested, either in hunting, game shooting, or fishing.
5. Urban environments: animals are encountered regularly due to coexistence in an urban location.

The impact of motorized vehicles such as cars, boats, helicopters and drones are well known and can initiate large FID from many species of animal or permanent resettlement of the individual, costing them territories, foraging opportunities, or reproduction (Smit and Visser 1993, Burger 1998, Rodgers and Schwikert 2002). Not only motorized vehicles, but recreational walking, biking, the presence of pets, or the noise from firearms may cause disturbance (Smit and Visser 1993, Rodgers and Smith 1995, 1997, Knight and Miller 1996, Lafferty 2001, Berger et al. 2007). Sometimes disturbances can cause relocations of an entire region, lasting sometimes only the day, but occasionally for much longer (Smit and Visser 1993). Lafferty (2001) found that snowy plovers (*Charadrius alexandrinus*) resting on a beach were disturbed by humans, dogs, and natural disturbances on average once every 27 minutes on the weekend, and once every 43 minutes on a weekday, and these disturbances negatively affected feeding rates of the birds.

The measuring of disturbance in an animal falls into four groups: avoidance responses such as escape behavior (AD, FID, DF); time budgets, where the amount of time spend in vigilance, comfort, or in foraging is calculated, or observations of increasing locomotion and aggression; physiological changes, or changes in breeding success; and finally quantifying fitness consequences (Tarlow and Blumstein 2007, Bateman and Fleming 2017). Approaches by humans and motorized vehicles have long been used to trigger AD and FID (Walther 1969, Smit and Visser 1993, Rodgers and Smith 1995, 1997), and the benefit of such measuring is that we can develop tourism and research programs and generate appropriate set-back distances for tourists from which to observe wildlife (Rodgers and Smith 1995, 1997, Fox and Madsen 1997, Burger 1998, Lafferty 2001, Rodgers and Schwikert 2002, Blumstein 2003, Blumstein et al. 2003, 2005, Fernández-Juricic et al. 2005). The number of human approachers can have an effect on the FID of prey species, with larger groups being perceived as a greater threat (Beale and Monaghan 2004b, Geist et al. 2005). Yet, as discussed previously, FID and stress responses tend to be lower in highly disturbed areas (urban areas) (Carrete and Tella 2010, Evans et al. 2010, van Dongen et al. 2015, Arroyo et al. 2017), which points to habituation, but also happens to be where predation risk is lowest due to lower predator densities (Valcarcel and Fernández-Juricic 2009, Díaz et al. 2013). Although habituation is one outcome, frequent fleeing caused by disturbance can incur energy losses through increased expenditure and the loss of intake opportunities, which lowers body condition and results in lowered fitness/survival, especially if feeding rates to offspring are affected by the disturbance (Frid and Dill 2002, Beale and Monaghan 2004b, Cresswell 2008, Arroyo et al. 2017). Disturbance may also cause a shift to sub-optimal habitats that are exposed to lower levels of disturbance (particularly through the displacement of less tolerant individuals), resulting in lower nesting success (Smit and Visser 1993, Frid and Dill 2002, Beale and Monaghan 2004b, Cresswell 2008, Wheeler et al. 2009, Arroyo et al. 2017, Rabdeau et al. 2021). When testing the effects of human disturbance on a range breeding colonial waterbirds, Rodgers and Smith (1995) found human disturbance caused egg and nestling mortality, nest abandonment, reduced nestling body mass, slow growth, and premature fledging. However, for individuals that are able to habituate more readily, they can experience greater increases in body condition than more flighty individuals (Rodríguez-Prieto et al. 2010).

Of particular interest to this thesis is the effects of human disturbance on penguin species. This has showed mixed results. Some penguin species habituate readily to benign human visitation, whearas other species sensitize to an extreme, resulting in lowered reproductive success and concerns for long-term population viability. Magellanic penguins, *Spheniscus magellanicus*, and African penguins, *Spheniscus dermersus,* from colonies exposed to tourist activities show fewer head turns (a threat behavior) and lower hormonal stress response than penguins from colonies less exposed to human presence, suggesting habituation (Van Heezik and Seddon 1990, Fowler 1999, Walker et al. 2006, Villanueva et al. 2012, Pichegru et al. 2016); however it is thought that this may be due to the re-location of shy individuals to less disturbed colonies (Fowler 1999). Gentoo penguins (*Pygoscelis papua*) also show habituation in response to human visitation: both baseline corticosterone and H:L ratios were lower in a more visited colony than a more protected colony, however penguins in the more visited colony had higher levels of heavy metals (Pb and Ni) suggesting indirect effects of human visitation (Barbosa et al. 2013). Little penguins (*Eudyptula minor*) sensitized to handling during research (Carroll et al. 2016), and in high-disturbance colonies also display higher vigilance and heart rate responses than those living in low-disturbance colonies (Schaefer and Colombelli-Négrel 2021). Yellow-eyed penguins (*Megadyptes antipodes*), are extremely sensitive to human presence; the careful approach of a wildlife photographer may provoke the same HR response as 10 minutes of handling (Ellenberg et al. 2013). At sites with higher human presence, yellow eyed penguins have higher baseline corticosterone, which is correlated with lower fledging weights, and since fledgling survival is positively associated with mass at fledging, this has resulted in long term population consequences (McClung et al. 2004, Ellenberg et al. 2007). Lower fledgling weights were found to be caused by interruptions of the parents returning with food, with many attempts being aborted, leading to over digestion of the stomach contents and the transfer of a smaller meal to the chicks when a successful transit finally occurs (French et al. 2019). Humboldt penguins (*Spheniscus humboldti*) are another species that displays intense sensitization to human presence; a person passing at a distance of 150 m can provoke a significant HR response (Ellenberg et al. 2006).

Physiological response to human presence can occur even without any overt changes in behavior (Nimon et al. 1996, Ellenberg et al. 2006, 2013). Snares penguins (*Eudyptes robustus*) showed significantly greater HR increases in response to a human approach than a natural disturbance and recovery times were significantly longer, and birds who were previously exposed to humans showed stronger responses than naïve birds (Ellenberg et al. 2012). Magellanic penguins, *Spheniscus magellanicus*, that are naïve to human presence show increased corticosterone responses (Fowler 1999), and the chicks of Magellanic penguins in disturbed areas show higher corticosterone stress responses, despite baseline levels remaining similar (Walker et al. 2005). Human passage through African penguin colonies, *Spheniscus demersus*, (<30 m from the colony edge) lead to temporary abandonment of nests and increased predation risk (Hockey and Hallinan 1981). Yet, human disturbance doesn't always have a sufficiently adverse effect; the reproductive success and breeding population size of Adélie penguins (*Pygoscelis adeliae*) were more strongly effected by environmental influences than human disturbance (Carlini et al. 2007), although another study found lower hatching success and chick survival in colonies subjected to recreational visits (Giese 1996). Similarly, tourism was not found to have an effect on the proportion of Gentoo penguins (*Pygoscelis papua*) that laid eggs, hatching success, or the proportion of single chick broods in colonies (Cobley and Shears 1999).

In king penguins, birds in zones of high human disturbance show attenuated HR responses to human approaches; however, there was no such attenuation for high intensity stressors such as capture (Viblanc et al. 2012a). This shows that king penguins have the potential to habituate to smaller human disturbance events (as compared to a capture), despite finding no behavioral sensitization or habituation in my studies. It is possible that I would have seen habituation or sensitization had the penguins been approached more often than three times over three days. Also, since BDM is a colony exposed to higher levels of human visitation, I have to wonder if the birds in BDM are the most tolerant to human approaches, while more sensitive birds with higher AD and FID have deserted the colony and settled elsewhere. Regardless, I can conclude that human approaches, while predation-free, are not innocuous, since they have effects on both individual behavior and physiology and carry the potential to negatively affect fitness.

3. Personality and fitness consequences

Animal personality is defined as any behavioral trait that is repeatable over time and contexts (Sih et al. 2004a, Réale et al. 2007, Dingemanse and Wright 2020). In Chapter 1, I found that FID and the decision to flee were repeatable over a period of three days. According to that definition, a personality trait was found in king penguins, at least over that short period of time in the context of incubating birds. However, in order to gain stronger support for these behaviors as personality traits, I would need to study these behaviors over a longer period of time, and in different contexts to see if the behavioral traits stay consistent for an individual (Dingemanse and Wright 2020). Because of logistic and time constraints in the field, only three approaches per individual were possible. It would be interesting to extend the sampling period to see if FID and the decision to flee remain repeatable for an individual over a breeding season, or if it extends as well to non-breeding periods such as during molt, waiting on the beach, or foraging at sea.

One complication to our study in Chapter 1 is that human approaches fell under two different aspects of personality: the evaluation of risk is associated with shyness-boldness gradient (i.e., FID), but human approaches could also be novel, falling under exploration-avoidance (Réale et al. 2007). When measuring FID over repeated approaches, an evaluation of the risk would be measured, but the focal animal could also habituate or sensitize as they become aware of the novel approach of a human experimenter. To account for this, a reaction norm approach would be helpful. A reaction norm measures the plasticity in the behavior across a given set of environments (Réale et al. 2007, Dingemanse et al. 2010, Dingemanse and Dochtermann 2013). The reaction norm could be flat, i.e., there is no variation or plasticity in the behavior (see Fig. 18A), consistently plastic across individuals (see Fig. 18B), or could be individually plastic (see Fig. 18C). In each of these situations, were we to consider the response of an animal to novel human approach, the relationship between boldness and exploration would be different. In A, there is no effect of exploration, only boldness, while in B, exploration and boldness are correlated, and in C, boldness and exploration are two separate traits. I propose that were the repeatability of king penguins tested again over a longer period (say over a breeding season), that the habituation or sensitization to human approaches be investigated in a reaction norm approach. This would separate the individual effects of boldness and exploration, and would illustrate how king penguins respond to growing experience (Réale et al. 2007).

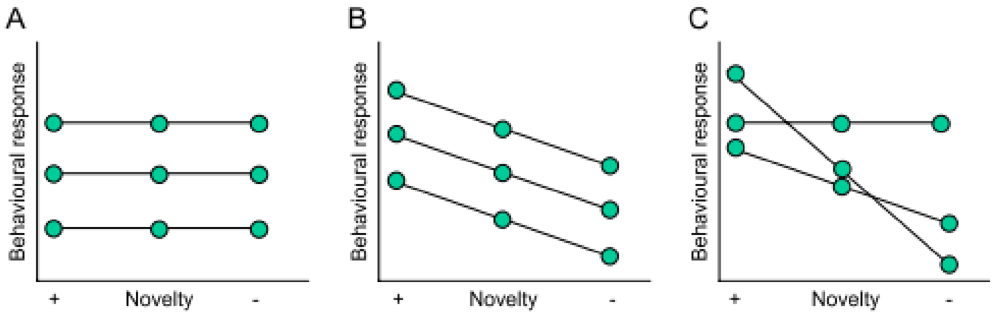

Figure 31. Examples of a reaction norm approach. Each dot represents a unique behavioral response, while the slope of each line represents the behavioral norm, or the amount of plasticity (variation) seen in the behavior. Each behavioral response could vary with the novelty of measurement. An example is the behavioral response to repeated approaches, to which the focal animal could habituate, sensitize, or show no response as exposure increases. In A, each individual has a unique personality but no plasticity, leading to a behavioral norm of 0. In B, each animal has a unique personality, but responds to the novelty of the situation in an identical manner. In C, the individuals respond differently to experience, leading to a different reaction norm for each individual. (Reproduced from Réale et al. 2007).

Once a personality is established, multiple behaviors can be compared in what is called a "behavioral syndrome". A behavioral syndrome a suite of correlated behaviors expressed within a given context (Sih et al. 2004b, Young et al. 2015). Common behaviors to correlate with boldness (i.e., FID) include: aggression (example: Petelle et al. 2013; Young et al. 2015; Moiron et al. 2019), vigilance (example: Edwards et al. 2013), or exploration (example: Carter et al. 2010, 2012; Couchoux and Cresswell 2012; Carrete and Tella 2017). Future studies on personality in king penguins could explore behavioral syndromes, for example are bold birds more aggressive, or shy individuals more vigilant? Shyer individuals were found to spend more time vigilant in eastern grey kangaroos, *Macropus giganteus* (Edwards et al. 2013). Or, is boldness related to exploratory behavior at sea? Birds could be equipped with GPS loggers and time depth recorders to test if bolder individuals explore the environment more at sea. A behavioral syndrome between boldness and exploration was found in captive coyotes, *Canis latrans* (Young et al. 2015), and young convict cichlids, *Amatitlania siquia* (Mazué et al. 2015). Bolder Namibian rock agamas were also found to be quicker to explore novel scenarios, which led to bolder males suffering greater rates of predation (Carter et al. 2010, 2012). Such possibilities remain to be explored in detail in penguins.

In addition to behavioral syndromes, personality measures can be similarly correlated to physiological measures in what is termed "coping styles". For instance, FID (boldness) could be correlated to stress hormone level or heart rates. Increased corticosterone or cortisol is associated with shyer responses, i.e., longer FIDs (Martin and Réale 2008, Atwell et al. 2012, Seltmann et al. 2012). Animals in better body condition cam afford to be more risk adverse (Seltmann et al. 2012, Moiron et al. 2019). Coping styles can be further separated into "reactive" copers, which have higher stress responses and respond to changes in their external environment, and "proactive" copers who respond less or not at all (Dingemanse et al. 2010, Bousquet et al. 2015). Proactive individuals seem to perform better in most learning tasks, while reactive individuals are expected to explore new environments more slowly but respond better to changes in their environments (Bousquet et al. 2015).

If personalities, in particular FID and boldness can correlate with other behaviors and physiological measures in behavioral syndromes and coping styles, it is logical to assume that selection could act on these suites of correlation resulting in differential fitness. One study that I wished to execute during my thesis, but for which I did not have enough time, was to explore the fitness benefits of boldness/shyness in breeding king penguins, chiefly among peripheral and central locations in the colony. Location in a colony is suggested as an explanation for uneven breeding success between center and edge nests of groups, for example in colonially breeding bank swallows, *Riparia riparia* (Hoogland and Sherman 1976), and yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Picman et al. 2002). In colonial orb-weaver spiders (*Meteperira incrassata*), larger spiders and females guarding egg sacs are more commonly found in the center of the colony and have higher reproductive success, despite the fact that prey availability is higher on the periphery, likely because predation risk is also significantly higher on the periphery (Rayor and Uetz 1990). Since central positions in king penguin colonies also experience lower predation pressure and higher breeding success, it is logical these positions are of higher fitness (Côté 2000, Descamps et al. 2005). Could there be an unequal distribution of bold and shy individuals across the colony? This would mean that the boldness/shyness of the individual may influence their breeding success. Bold individuals flee at shorter distances and therefore have fewer disturbances to parental care and may have higher fitness. For example, nest visit frequency was shown to increase nest failure and reduce productivity of shy female Montagu's harrier (*Circus pygargus*), but not bold ones (Arroyo et al. 2017). This is because, when disturbed, shy individuals left their nests exposed to predation, inclement weather, or low levels of necessary parental care (Arroyo et al. 2017). However, another study showed that hatching success in Eurasian curlews (*Numenius arquata*) was highest in nests where the parents left at intermediate FIDs (de Jong et al. 2013). In this study, I propose exploring the fitness benefits of boldness/shyness between central and peripheral locations in the colony by measuring chick growth rates and survival to thermal emancipation. After thermal emancipation, the adult is no longer involved directly in antipredator defenses of the offspring.

4. Future perspectives

Throughout the process of this thesis, many more questions arose than could be answered in such a short period of time. Many of these I have already highlighted in the previous sections, as relevant, but there remain several other paths that could be explored. I will discuss these further below.

Vigilance behavior, despite being commonly and well-studied in the literature, was not included in this thesis. There are many questions that remain to be answered about vigilance in king penguins. Does vigilance vary with location in the colony, as predation pressure is highest on the periphery (Côté 2000, Descamps et al. 2005)? Does vigilance increase at dawn and dusk when the natural predators of king penguins are most active (Le Bohec et al. 2003)? In the literature, it is a common finding for vigilance to increase during periods of the day when the risk of predation is higher (Bednekoff and Ritter 1994, Burger and Gochfeld 1994, Matson et al. 2005, Li et al. 2012, Edwards et al. 2013, Roche and Brown 2013, Boujja-Miljour et al. 2018). Does vigilance reduce in colonies/groupings of king penguins according to the group-size effect (Pulliam 1973, Elgar 1989, Quenette 1990, Lima 1995)? While the group-size effect has been well examined in social groupings of other species, it is rather understudied in colonial species. In addition, it has also been found that vigilance directed towards conspecifics increases when social demands increase (Roberts 1988, Quenette 1990, Carter et al. 2009, Edwards et al. 2013), such as in colony life. It’s possible overall vigilance in king penguins may increase when they are in their colonies due to increased social vigilance. Does vigilance vary according to life history stage? In the literature, vigilance is usually increased in animals with young present (Burger and Gochfeld 1994, Childress and Lung 2003, Carter et al. 2009, Li et al. 2009). It’s possible that there may be an increase in vigilance behavior in incubating and brooding king penguins. This may be counterintuitive because in Chapter 2 reproductive birds were found to have lower AD than non-reproductive birds. However, the relationship between vigilance and AD is poorly tested and thus remains unclear. It is frequently assumed and rarely tested that vigilance behavior and AD should be correlated (example: Uchida et al. 2019). However, this has only been tested in two studies to date, one of which finding no correlation between AD and vigilance behavior (Fernández-Juricic and Schroeder 2003, Tätte et al. 2019). I suggest testing for a correlation between vigilance behavior and AD in king penguins.

One behavior that merits further attention is the use of mobbing in king penguins. From personal observation, unintentional mobbing occurs when the targeted prey flees towards neighboring individuals in the colony. These neighbors proceed to attack not only the targeted prey individual, but also the approaching threat. Mobbing is thought to confuse and distract the predator through the presence of many aggressive individual prey preventing the predator from selecting and attacking just one individual, thus reducing predation risk and lowering the chance of a successful predation attempt (Sordahl 1990). While I don't believe mobbing is an active tactic in by king penguins, like it is in meerkats, *Suricata suricatta* (Graw and Manser 2007), bank swallows, *Riparia riparia*, (Hoogland and Sherman 1976), cliff swallows, *Hirundo pyrrhonata*, (Brown and Brown 1987), and white-tailed and black-tailed prairie dogs, *Cynomys leucurus* and *Cynomys ludocivianus,* (Hoogland 1981), I do think that group aggressiveness towards predators in king penguins merits further exploration. Although this does not directly relate to flight behaviors, this is something that could be tested both for non-breeding adults, breeding adults in the colony, and chicks in creches.

One result in this thesis that regularly appeared but was not directly tested was differences in AD, FID, and DF in the various zones of BDM. It remains unclear why different zones would have different levels of antipredator behaviors. It's possibly due to different levels of human disturbance, different levels of predation risk (uneven distribution of predators), differences in bird density, topography, or angle of approach of predators. This is one aspect that could be explored in more detail, for instance by measuring predator frequentation and predation by predators through visual observation.

Finally, it is well established that the repeatability of a trait sets the upper limit for its heritability (Falconer and Mackay 1996, Dingemanse et al. 2002, Van Oers et al. 2004, Réale et al. 2007, Lartigue et al. 2021). I would be greatly interested to see if there was a correlation between parent and offspring AD, FID, and DF – and partition the variance in antipredator behavior explained by additive genetic and environmental factors. For example, Mazué et al. (2015) found repeatable and heritable individual differences in boldness and exploratory behaviors in the convict cichlid fish, *Amatitlania siquia*. As reproductive pairs and chicks can be easily followed to fledging, the heritability of boldness behavior is readily testable. In a long-term dataset, we have already collected AD and FID for chicks for many years, and as part of my field work, I started performing behavioral scans on chicks in the hopes that someday chick behavior may be tested against their parents' behaviors. Further, previous experiments on cross-fostering have been done in this species, allowing to separate early-environmental/genetic effects from environmental/rearing effects (Viblanc et al. 2020), and such approaches could be used to better understand the determinism of antipredator behavior by comparing chick and parental (genetic or foster) responses to human approaches.

5. What I learned from this PhD: challenges, successes, and personal growth

As with any great work, this thesis came with its own set of challenges that needed to be met. First, and most likely, foremost on people's minds is the impact COVID had on this thesis. COVID happened directly in the middle of this thesis, and while it had great personal impact on me, it did not greatly impact the logistics of the thesis or the collection of data. Much of this thesis was based around organizing and analyzing previous datasets, which could be done as easily from home as from the office. And with the advances in video technology (Zoom, Microsoft Teams, WhatsApp), meetings with supervisors and colleagues were easy to arrange. The largest impact COVID had was on my personal social life and wellbeing. I was quarantined in an 18m^2 apartment for close to six months and greatly missed seeing people, exploring France, and going for walks in nature with my dog. But as with all things, hard times passed and I was once again able to enjoy these things. I gained great perspective on how to socialize from a distance, and how it is always possibly to find proactive solutions that will make work happen as it should.

Otherwise, there were two other challenges that had to be faced during this thesis. The first was adjusting to life long-term in a foreign country with different culture and language. Initially it was hard to establish independent life, and I struggled with isolation and making friends. But with persistence and help from friends and supervisors, I was able to set up a comfortable lifestyle. I branched out and joined numerous social groups in order to help with the social isolation. And through studying the language daily, I was able to bring myself a measure of independence. I learnt the importance of persistence and daily effort in bringing about a satisfying personal life. Yet, the hardest struggle of all was with my mental health. I suffer from major depressive disorder (and have for many years) and it has large impacts on my day-to-day functioning and well-being. In dealing with my illness, I've learned the importance of breaking down large, insurmountable tasks into smaller manageable objectives. I also can see the benefit of how doing a small amount of work each day can lead to large accomplishments in the long term, as is evidenced by the completion of this thesis. It also can't be understated how much personal relationships contribute to wellbeing. My illness has pointed out to me one of my greatest strengths is determination and persistence, and my greatest blessing is the people I've been lucky enough to meet.

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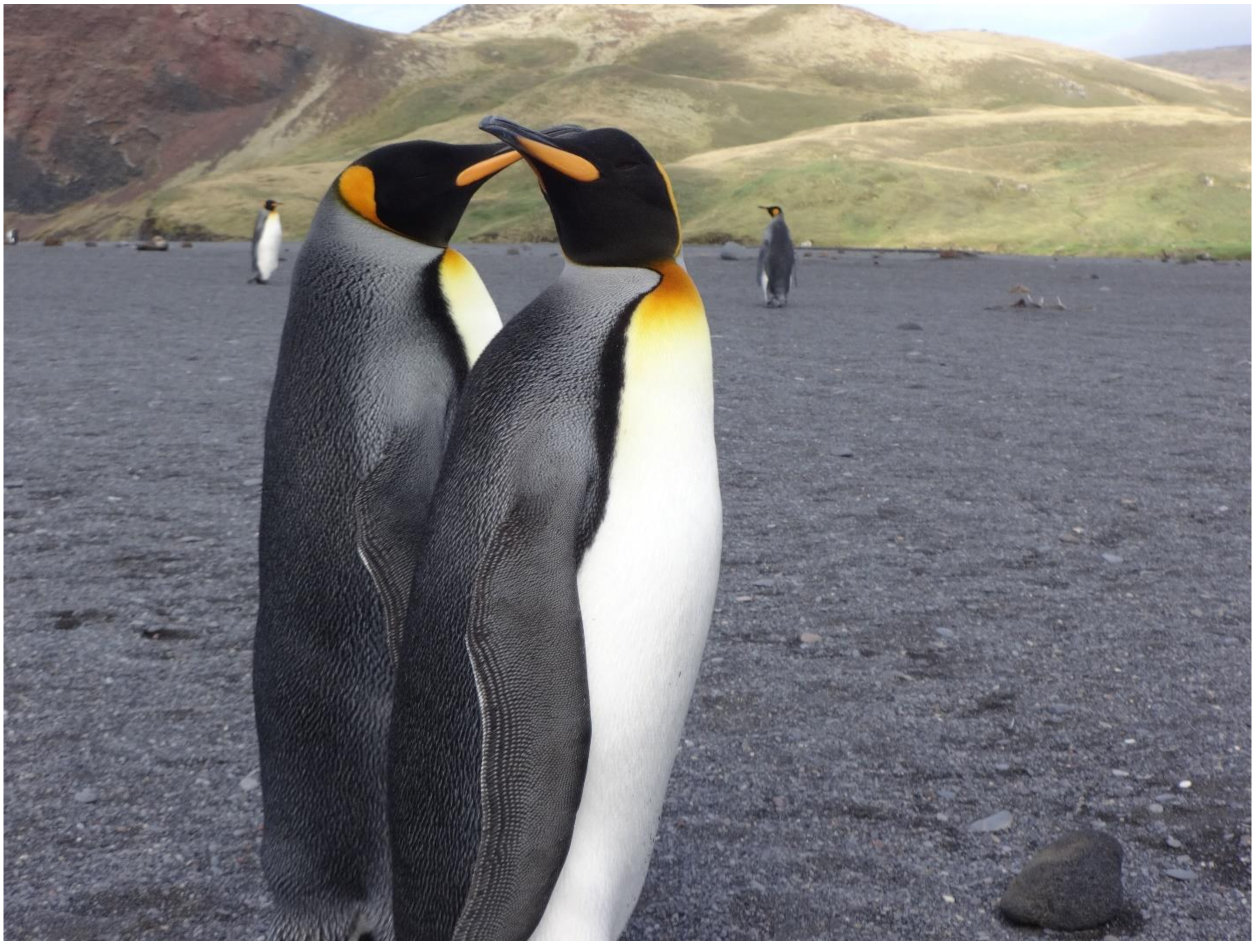
Appendices



Appendix 1

Distribution of Alert Distance and Flight Initiation Distance

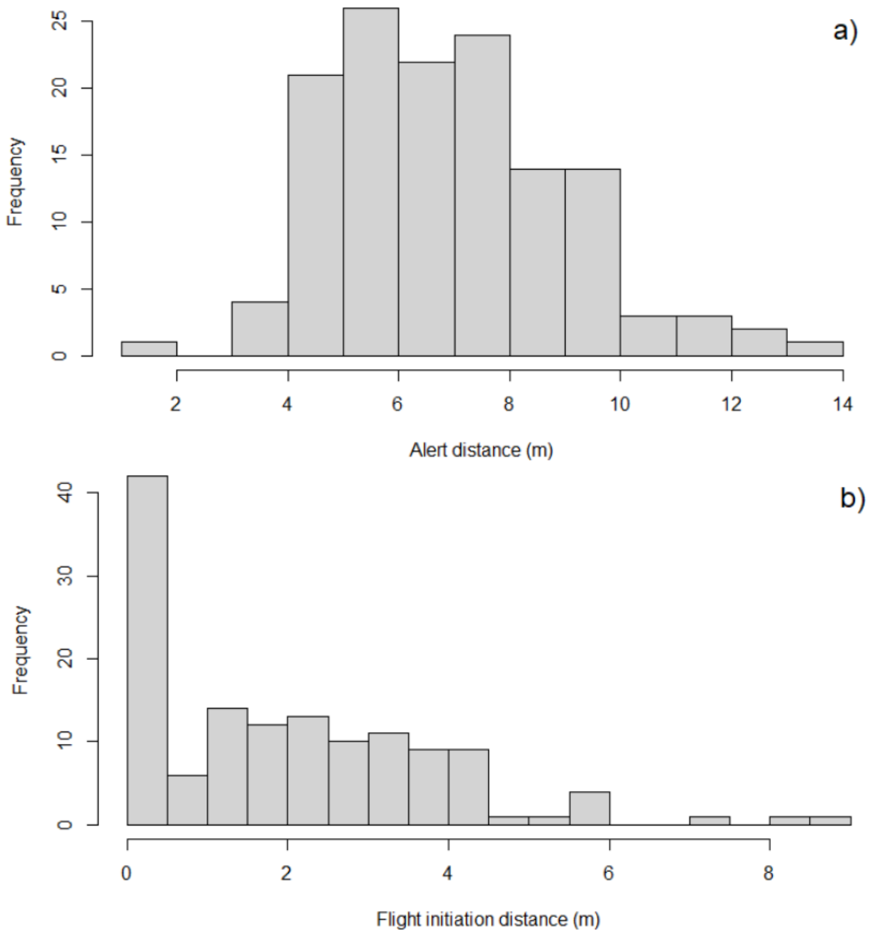


Figure 32. Histogram distributions of a) alert distance and b) flight initiation distance seen in incubating king penguins (*Aptenodytes patagonicus*) resulting from all collected approaches (n=135 observations, N = 47 individuals).

Variation in weather conditions

Variation in weather conditions between our different bird approaches within the two colonies of la Baie du Marin (BDM) and Jardin Japonais (JJ). The marginal estimated means of Linear Mixed Models are presented where the dependent variable was either weather PC1 or weather PC2. The independent variables were colony, approach number and the interaction between both variables, and the random term was bird ID.

Weather PC1 (temperature and sun)

We found a significant effect of the colony x approach (LMM; $F_{2,87.34} = 36.96$, $P < 0.0001$) interaction on weather PC1. Post-hoc analyses using Tukey HSD ('emmeans' package in R) indicated that in each colony all 3 approaches differed in terms of their average weather conditions.

Table 1. Estimated marginal means and 95% CI for weather PC1.

BDM colony		**Marginal mean ± SE**	**CI**
Approach	1	1.442 ± 0.199	[1.048 – 1.837]
	2	0.759 ± 0.208	[0.347 – 1.171]
	3	-1.283 ± 0.213	[-1.705 – -0.861]
JJ colony			
Approach	1	1.356 ± 0.204	[0.953 – 1.759]
	2	-1.874 ± 0.204	[-2.276 – -1.471]
	3	-0.562 ± 0.208	[-0.974 – -0.150]

Table 2. Contrasts between approach levels (Tukey HSD) for weather PC1.

BDM colony		**Estimate ± SE**	**df**	**t**	**P**
Contrast	1-2	0.684 ± 0.283	87.6	2.412	0.0467*
	2-3	2.725 ± 0.287	88.9	9.488	<0.0001*
	2-3	2.041 ± 0.293	86.3	6.969	<0.0001*
JJ colony					
Contrast	1-2	3.230 ± 0.283	85.0	11.416	<0.0001*
	2-3	1.918 ± 0.286	86.2	6.699	<0.0001*
	2-3	-1.312 ± 0.286	86.2	-4.581	<0.0001*

Weather PC2 (wind and rain)

We found a significant effect of the colony x approach (LMM; $F_{2,129} = 86.26$, $P < 0.0001$) interaction on weather PC2. Post-hoc analyses using Tukey HSD ('emmeans' package in R) indicated that in each colony most approaches differed in terms of their average weather conditions.

Table 3. Estimated marginal means and 95% CI for weather PC2

BDM colony		**Marginal mean ± SE**	**CI**
Approach	1	-0.730 ± 0.100	[-0.929 – -0.531]
	2	0.662 ± 0.105	[0.454 – 0.870]
	3	0.212 ± 0.108	[-0.001 – 0.424]
JJ colony			
Approach	1	0.501 ± 0.103	[0.298 – 0.704]
	2	0.663 ± 0.103	[0.460 – 0.866]
	3	-1.284 ± 0.105	[-1.492 – -1.077]

Table 4. Contrasts between approach levels (Tukey HSD) for weather PC2

BDM colony		**Estimate ± SE**	**df**	**t**	**P**
Contrast	1-2	-1.392 ± 0.145	87.6	-9.582	<0.0001*
	2-3	-0.942 ± 0.147	89.0	-6.402	<0.0001*
	2-3	0.450 ± 0.150	86.4	2.998	0.0098*
JJ colony					
Contrast	1-2	-0.163 ± 0.145	85.1	-1.120	0.5044
	2-3	1.785 ± 0.147	86.4	12.162	<0.0001*
	2-3	1.947 ± 0.147	86.4	13.269	<0.0001*

Post-hoc power analyses for detecting statistically significant repeatability of Alert Distance

We used the PAMM package in R (Martin et al. 2011) to evaluate the variance in individual-specific intercepts of our data set, and simulate how much data would have been needed to detect significant repeatability in AD (viz. statistically significant differences in individual intercepts). To this end, we used the variance components estimated from our final repeatability model for AD, controlling for weather PC1. In our case:

- Variance component for the intercept, VI = among-individual variance = $\sigma^2_\alpha = 0.586$
- Residual variance, VR = within-individual variance = $\sigma^2_\varepsilon = 3.466$

We then ran 1000 simulations for samples sizes ranging rom 20 to 200 individuals and 3 to 10 repeated approaches per individual. From the plots below, we can see that with 3 repeated approaches per individual (graphs A and B), we would have needed to approach 140 birds to reach a power of 0.8 and a significance threshold of 0.05. Alternatively, by approaching 47 birds as we did, we would have needed to approach birds 6 times to reach a similar power of 0.8 and a significance threshold of 0.05. Hence, we would have needed to double the number of approaches per bird in our study, or almost triple the number of birds approached.

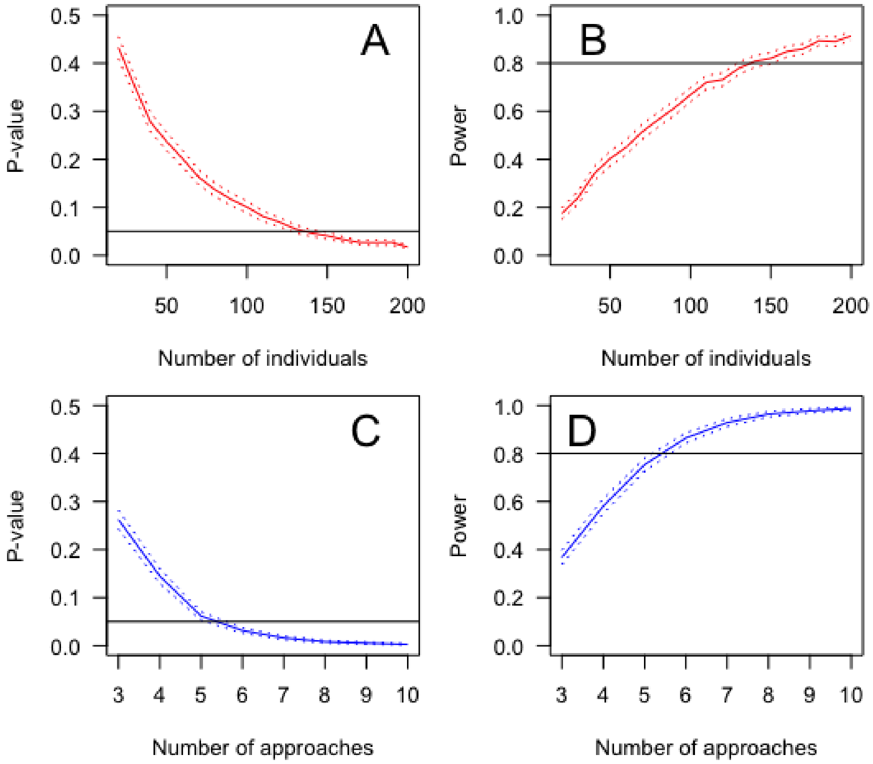


Figure 33. Simulated runs (1000 simulations) used to determine the number of individuals or the number of approaches needed to reach a statistical power of 0.8 ($P < 0.05$) for AD repeatability when considering: (A and B) 3 approaches per individual, or (C and D) 47 birds.

Reference:

Martin, J. G., Nussey, D. H., Wilson, A. J., & Reale, D. (2011). Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. *Methods in Ecology and Evolution*, *2*(4), 362-374.

Tracey HAMMER

Anti-predator behaviors: Sources of variation and reproductive consequences

Résumé

Les animaux utilisent des comportements tels que la vigilance ou la fuite pour faire face à la menace de la prédation. J'examine plusieurs comportements anti-prédateurs : la Distance d'Alerte (AD), la Distance de Fuite (FID), et la Distance Fuite (DF). Tous ces comportements sont connus pour être influencés par le niveau de risque évalué par la proie, et la fuite ne devrait être entreprise que lorsque les avantages de la fuite sont égaux aux coûts du départ. Dans le chapitre 1, AD et FID sont évalués en tant que traits de personnalité. Dans le chapitre 2, j'ai exploré l'effet de la vie en groupe et des distractions sociales sur les comportements anti-prédateurs (AD, FID et décision de fuir). Et enfin, au chapitre 3, j'ai comparé les réponses comportementales anti prédatrices entre les différentes étapes de l'histoire de la vie. Les résultats montrent que le comportement de vol des manchots royaux est complexe et expliqué par une série d'hypothèses mutuellement non exclusives.

Mots clés :
Manchot royal (*Aptenodytes patagonicus*), Distance de alerte, Distance de Fuite, Distance fuite, densité du groupe, traits de personnalité, répétables, hypothèse de la valeur du couvain, reproduction investissement, défense de la progéniture parentale

Résumé en anglais

Animals use behavior such as vigilance or flight in order to cope with the threat of predation. I look at several antipredator behaviors: Alert Distance (AD), Flight Initiation Distance (FID), the decision to initiate flight, and Distance Fled (DF). All of these behaviors are known to be influenced by the amount of risk assessed by the prey, and flight should only be undertaken when the benefits of fleeing equal the costs of leaving. In Chapter 1, AD and FID are evaluated as personality traits. In Chapter 2, I explored the effect of group living and social distractions on anti-predator behaviors (AD, FID, and the decision to flee) by testing four different hypotheses. And finally, in Chapter 3, I compared antipredator behavioral responses between different life history stages, and test the brood value hypothesis. The results show that king penguin flight behavior is complex and explained by a range of mutually non-exclusive hypotheses.

Keywords :
King penguin (*Aptenodytes patagonicus*), Alert Distance, Flight Initiation Distance, Distance Fled, social density, personality trait, repeatability, brood value hypothesis, parental investment, parental offspring defense