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Réponses aux contraintes de reproduction chez le manchot Adélie

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REPONSES AUX CONTRAINTES DE REPRODUCTION CHEZ LE MANCHOT ADELIE

Thèse présentée pour l'obtention du titre
de Docteur de l'Université de Strasbourg
par

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“Les pingouins sont des oiseaux qui, au lieu d'ailes, ont deux nageoires et deux grosses pattes, sur lesquelles ils marchent debout et avec lesquelles ils fouissent la terre pour faire leurs nids. Ils sont de la grosseur d'un cormoran et plus, ont le ventre blanc et le dos noir, la tête fort grosse et le bec comme celui d'un corbeau. Le matin, ils se mettent à la mer, où ils nagent entre deux eaux et ne mangent que du poisson ; le soir, ils reviennent à leurs nids. Ils n'ont point du tout le goût de chair, et je les tiens pour des poissons emplumés.”

Amiral Augustin de Beaulieu
Mémoires d'un voyage aux Indes orientales, 1619-1622 : un marchand normand à Sumatra

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Articles

Articles inclus dans ce mémoire

1. **Beaulieu M.**, Raclot T., Le Maho Y., Ropert-coudert Y., Ancel A. (2009) Can a handicapped parent rely on its partner? An experimental study within Adélie penguin pairs. *Animal Behaviour* 78: 313-320. doi: 10.1016/j.anbehav.2009.05.006
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5. **Beaulieu M.**, Ropert-Coudert Y., Ancel A., Criscuolo F. Foraging in an oxidative environment: relationship between $\delta^{13}C$ values and oxidative status in Adélie penguins. *Proceedings of the Royal Society B* (sous presse)
6. **Beaulieu M.**, Spée M., Chastel O., Le Maho Y., Lacroix A., Ancel A., Raclot T. Prolactin and the regulation of foraging trip duration in Adélie penguins? (soumis)
7. **Beaulieu M.**, Reichert S., Le Maho Y., Ancel A., Criscuolo F. Controlling for oxidative stress and saving telomere length: mechanisms to avoid the fitness cost in long-lived birds? (soumis)
8. **Beaulieu M.**, Ropert-Coudert Y., Le Maho Y., Lazin D., Ancel A. Diving adaptability of Adélie penguins with different diving capacities, in response to environmental constraints (soumis)

Articles présentés en annexe

1. **Beaulieu M.**, Thierry A.M., Raclot T., Le Maho Y., Ropert-coudert Y., Gachot-Neveu H., Ancel A. (2009) Sex-specific parental strategies according to the sex of offspring in the Adélie penguin. *Behavioral Ecology* 20: 878-883 doi: 10.1093/beheco/arp076
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8. Nesti I., Ropert-Coudert Y., Kato A., **Beaulieu M.**, Focardi S., Olmastroni S. Diving behaviour over the complete chick-rearing period in a fast-ice area. (en révision)
9. Ropert-Coudert Y., Kato A., Wilson R.P., **Beaulieu M.** Short and long trips... and everything in between: regulation of foraging trip duration in seabirds (soumis)
10. Ancel A., **Beaulieu M.**, Le Maho Y., Gilbert C. Why is emperor penguins' courtship so long? (en préparation)
11. Spée M., Marchal L., Dervaux A., Thierry A.M., Lazin D., Le Maho Y., **Beaulieu M.**, Raclot T. Exogenous corticosterone mimics a late stage of fasting in Adélie penguins (en préparation)
12. Spée M., Dervaux A., Lazin D., Chastel O., Le Maho Y., **Beaulieu M.**, Raclot T. Hormonal control of nest abandonment in breeding Adélie penguins (en préparation)
13. Spée M., Thierry A.M., Marchal L.., Lazin D., Le Maho Y., **Beaulieu M.**, Raclot T. Is corticosterone involved in nest abandonment in free-ranging Adélie penguins (en préparation)

Présentations

Présentations orales

1. **Beaulieu M.**, Spée M., Lazin D., Le Maho Y., Ancel A, Raclot T. Ecophysiological response of Adélie penguins facing an experimental increase in breeding constraints. 7th European Ornithologists' Union Conference. Août 2009, Zurich, Suisse.
2. **Beaulieu M.**, Dervaux A., Thierry A.M., Lazin D., Le Maho Y, Ropert-Coudert Y., Spée M., Raclot T, Ancel A. Ecophysiological response of Adélie penguin parents facing contrasting timing of sea-ice retreat. Xth SCAR (Scientific Committee on Antarctic Research) International Biology Symposium, Juillet 2009, Sapporo, Japon. Présentation récompensée d'un "Student / Early Career Award".
3. Gilbert C., **Beaulieu M.**, Le Maho Y., Ancel A. Do emperor penguins huddle at unison during the pairing period? 3ièmes journées du CNFRA (Comité National Français pour le Recherche Antarctique) Octobre 2008, Paris, France.
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Communications affichées

1. Spée M., **Beaulieu M.**, Marchal L., Dervaux A., Lazin D., Thierry A.M., Le Maho Y., Raclot T. Involvement of corticosterone in the refeeding signal using an experimental approach in fasted captive and free-ranging Adélie penguins. Xth SCAR International Biology Symposium, Juillet 2009, Sapporo, Japan.
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I. PICASO: Penguins as Indicators of Climate Anomalies in the Southern Ocean. Xth SCAR International Biology Symposium, Juillet 2009, Sapporo, Japon.

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INTRODUCTION

Introduction

I – Contexte

Les êtres vivants disposent de ressources limitées qu'ils doivent allouer aux différentes fonctions biologiques. Ainsi, sous certaines circonstances, une fonction ne pourra être privilégiée qu'au détriment d'une autre (Stearns 1992). Le conflit entre reproduction et maintenance[1] en est l'un des meilleurs exemples. Ainsi une augmentation de l'énergie allouée à la reproduction ne peut se faire qu'au détriment des chances de survie et de la fécondité à venir (**valeur reproductive résiduelle**). Par conséquent, les organismes, en fonction de leurs **traits d'histoire de vie**[2], doivent adopter des **décisions**[3] optimisant leur **valeur sélective** ("genotypic fitness"), c'est à dire leur capacité à transmettre leur patrimoine génétique aux générations futures (Williams 1966, Stearns 1992), et donc augmentant leur **aptitude phénotypique** ("fitness"), c'est à dire leur capacité à survivre et à produire des descendants matures.

I.1 – Définitions

L'investissement nécessaire à la reproduction se décompose en investissement sexuel et investissement parental. L'**investissement sexuel** représente l'énergie consacrée à rechercher et obtenir un partenaire et à éloigner les rivaux. L'investissement parental est défini en fonction des conséquences que les soins parentaux induisent sur la fitness des parents ; il correspond à la part de ressource parentale investie sous forme de temps ou d'énergie dans les soins parentaux apportés aux jeunes (*i.e.* la **dépense parentale** ; Cézilly & Danchin 2005) mais qui empêche les parents d'investir dans d'autres composantes de leur fitness (Clutton-Brock 1991). D'un côté, une augmentation de l'investissement parental permet d'améliorer le nombre et la qualité des descendants, mais de l'autre côté, cette augmentation peut être délétère à la maintenance et à la survie de l'adulte ainsi qu'à sa descendance future. L'**investissement parental** se définit donc comme toute dépense parentale qui est bénéfique pour la progéniture aux dépens des chances du

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[1] **Maintenance** : ensemble des mécanismes permettant la conservation des fonctions vitales de l'organisme.
[2] **Traits d'histoire de vie** : ensemble des caractères impliqués dans la survie et la reproduction.
[3] **Décision** : adoption d'un comportement parmi plusieurs comportements possibles en fonction des coûts et des bénéfices associés.

parent de se reproduire dans l'avenir (Trivers 1972). L'impact négatif de l'investissement parental sur les chances de survie et de succès reproducteur à venir représente le **coût de la reproduction** (Williams 1966). Ainsi les individus réussissant à trouver le meilleur compromis entre dépense parentale, augmentant la survie de leur progéniture, et le maintien de leur propre valeur reproductive résiduelle, devraient être favorisés en termes de sélection.

I. 2 – Conflits sexuel et intergénérationnel

Dans le règne animal, les soins parentaux peuvent être apportés par la femelle uniquement (chez 90 % des espèces de mammifères), le mâle uniquement (chez les amphibiens et les poissons notamment) ou les deux à la fois (chez 90 % des espèces d'oiseaux ; Kokko & Jennions 2008). Chez les **espèces biparentales**[4], mâles et femelles cherchent à maximiser leur fitness. Un parent aura donc tout avantage à ce que l'autre parent assume la plus grande partie des coûts associés à la production des jeunes (Houston *et al.* 2005). Un conflit peut alors apparaître entre les deux sexes si le compromis optimal d'un parent ne correspond pas au compromis optimal de l'autre parent. De cette divergence est née la notion de **conflit sexuel** (Trivers 1972) : mâles et femelles sont sélectionnés pour minimiser leur investissement dans la reproduction actuelle mais sont néanmoins obligés de coopérer pour mener à bien cette reproduction.

Par ailleurs, pour assurer sa survie et celle de sa progéniture, un parent se doit de confronter ses propres besoins aux besoins de sa progéniture. Or il existe également un conflit d'intérêt entre parents et jeunes sur le niveau optimal de soins : ce qu'un parent donne à sa progéniture, il le perd pour sa propre maintenance. De cette opposition entre intérêts des parents et intérêts des jeunes est née la notion de **conflit intergénérationnel** (Trivers 1974). Le conflit tournera à l'avantage des jeunes si ceux-ci parviennent à manipuler l'investissement de leurs propres parents en augmentant la durée ou l'intensité des soins parentaux (*via* l'intensité de leurs sollicitations par exemple ; Kitaysky *et al.* 2001, Quillfeldt 2002) parvenant ainsi à obtenir un niveau d'investissement parental supplémentaire qui diminuera en contrepartie les chances de survie des parents.

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[4] **Espèces biparentales** : espèces chez qui le succès reproducteur est tributaire des soins apportés par les deux parents.

II – Les Oiseaux : modèles d'étude de l'investissement parental

Les oiseaux ont pour intérêt de couvrir un large spectre quant au mode et à l'importance des soins prodigués aux poussins. Certaines espèces appartenant aux familles des Mégapodidés ou des Cuculidés abandonnent leurs œufs dès la ponte et par conséquent ne prodiguent aucun soin aux jeunes (Roper 1983, Dearborn *et al.* 2009). Hormis ces cas particuliers, les soins aux poussins chez les oiseaux vont du simple gardiennage chez les espèces nidifuges[5], à l'apport de chaleur et au nourrissage chez les espèces nidicoles[6]. De plus, pour une grande majorité d'espèces (90%), mâles et femelles s'investissent dans l'incubation et/ou l'élevage des jeunes (Kokko & Jennions 2008).

Chez les oiseaux, le comportement parental comprend deux composantes principales : la présence au nid et la prospection alimentaire. Chez les espèces nidifuges, cette phase au nid ne se limitera qu'à l'incubation alors que chez les espèces nidicoles, cette phase se poursuivra pendant l'élevage des poussins au moins jusqu'à ce que ces derniers deviennent thermiquement indépendants. Cela implique chez les espèces biparentales, qu'il y ait constamment au moins un des deux parents sur le site de reproduction pendant des périodes plus ou moins longues (jusqu'à plusieurs mois chez le manchot empereur *Aptenodytes forsteri* ; Prévost 1961). Or du fait de la distance séparant les zones de recherche alimentaire et le site de reproduction, les périodes au nid sont généralement synonymes de jeûne pour les parents. Pour résoudre ce problème, deux stratégies sont possibles chez les espèces biparentales : (1) un des deux parents reste constamment sur le nid et est approvisionné par son partenaire (ex : rapaces (Donazar *et al.* 1992), moucherolles (Morton & Pereyra 1985)) ou (2) les deux parents alternent successivement présence sur le nid et prospection alimentaire (ex : oiseaux marins ; *e.g.* Tveraa *et al.* 1997). Ces deux alternatives montrent bien l'interdépendance existant entre les deux parents d'un même couple qui se doivent donc de coordonner leurs comportements de façon à assurer leur succès reproducteur.

Dans le cas où les parents alternent présence au nid et prospection alimentaire, le parent de retour sur le nid aura dû accumuler suffisamment de réserves pour jeûner jusqu'au retour de son partenaire, sous peine qu'il abandonne la reproduction en cours si ces réserves corporelles venaient à atteindre un seuil critique pour sa survie (Ancel *et al.* 1998, Groscolas *et al.* 2008). A

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[5] **Espèces nidifuges** : espèces chez qui les poussins sont indépendants dès l'éclosion (i.e. mobiles et émancipés thermiquement) ; principalement Ansériformes et Galliformes.

[6] **Espèces nidicoles** : espèces chez qui les poussins sont dépendants des parents après l'éclosion (ex : Passériformes, Sphénisciformes).

l'inverse, le temps dévolu à la recherche alimentaire d'un parent se trouve limité dans la mesure où il doit correspondre au temps de jeûne que son partenaire resté au nid est capable de supporter (Tveraa *et al.* 1997).

III – Régulation de l'investissement parental

Le comportement parental peut prendre de multiples facettes en fonction des espèces, des populations, du sexe, des individus et peut différer chez certains individus à différents moments de leur vie ou au cours d'une même saison de reproduction. Dans cette partie, nous passons en revue l'ensemble des facteurs susceptibles de moduler le niveau d'investissement parental.

III. 1 – Facteurs extrinsèques au parent

Niveau des ressources disponibles

Du point de vue d'un prédateur, la qualité d'un habitat peut se définir par l'adéquation entre ses besoins et le niveau de ressources disponibles dans son environnement. Trois facteurs principaux sous-tendent cette disponibilité en ressources : (1) la saisonnalité ("timing"), (2) l'abondance, et (3) l'accessibilité (Durant *et al.* 2007). Ainsi, la saison de reproduction coûteuse en terme d'énergie coïncide généralement avec une augmentation des ressources disponibles dans l'environnement. Cela permet aux parents de trouver suffisamment de nourriture pour se nourrir eux-mêmes et, dans le cas où les jeunes ne sont pas indépendants, pour nourrir leur progéniture.

Dans la situation où les ressources seraient insuffisantes relativement aux besoins imposés par la reproduction, plusieurs alternatives s'offrent aux parents : ils peuvent (1) ne pas se reproduire de façon à minimiser leurs besoins énergétiques et attendre la prochaine saison de reproduction potentiellement plus faste (Drent & Daan 1980), (2) décaler leur saison de reproduction de façon à ce que leurs besoins liés à la reproduction correspondent au pic de disponibilité alimentaire (Barbraud & Weimerskirch 2006), (3) se reproduire sur la même base temporelle au risque de ne pas disposer de suffisamment de ressources ou alors en changeant la nature de leurs ressources (Croxall *et al.* 1999, Miller & Trivelpiece 2008, Nicol *et al.* 2008). Dans la dernière situation, les prédateurs ne pourront changer de proies que s'ils sont capables de mettre en place de nouvelles stratégies de prospection alimentaire.

Enfin, dans le cas où les individus se reproduisent malgré des ressources alimentaires insuffisantes, trois scénarii sont envisageables concernant leur condition corporelle : (1) les parents maintiennent leur condition corporelle constante en diminuant le niveau de nourrissage de leur progéniture, (2) les parents maintiennent leur niveau de nourrissage constant aux dépens de leur propre condition corporelle, (3) à la fois la condition corporelle de l'adulte et le niveau de nourrissage sont affectés (Gaston & Hipfner 2006).

Il faut également noter que la disponibilité en ressources va également fluctuer en fonction du nombre d'individus dépendants des mêmes ressources simultanément. Ainsi le comportement parental et le succès reproducteur vont également être tributaires du niveau de compétition inter- et intra-spécifique dans un milieu donné. Un exemple est donné par une étude portant sur le grimpereau des bois *Certhia familiaris* et ayant montré que le succès reproducteur de cette espèce était diminué lorsque ceux-ci entraient en compétition avec des fourmis rousses *Formica rufa* dépendantes des mêmes ressources alimentaires (Aho *et al.* 1999).

Risque de prédation sur les parents

L'approvisionnement régulier des poussins impose aux parents d'effectuer constamment des allers-retours entre la colonie et les zones de prospection alimentaire, ce qui augmente leur probabilité de rencontre avec leurs prédateurs. Par conséquent, la pression de prédation exercée sur les parents est susceptible de moduler leur niveau d'investissement dans la reproduction et il est probable que pour privilégier leur survie, les parents diminuent le niveau de soins apportés à leur progéniture lorsque le risque de prédation augmente. Ainsi il a été montré que les puffins des Anglais *Puffinus puffinus* approvisionnaient moins leurs poussins lorsqu'ils étaient davantage exposés au risque de prédation (Riou & Hamer 2008).

Demande de la progéniture

Les besoins de la progéniture diffèrent en fonction de l'âge des jeunes. Ainsi, dans un premier temps, les jeunes auront des besoins alimentaires faibles du fait de leur petite taille, mais auront besoin de la présence des adultes pour les protéger et leur apporter de la chaleur jusqu'à ce qu'ils soient thermiquement indépendants. A l'opposé, une fois émancipés thermiquement, les jeunes, plus gros, auront de moins en moins besoin de leurs parents pour leur fournir de la chaleur et les protéger mais auront des besoins alimentaires quantitativement de plus en plus importants. Par conséquent, les parents se doivent d'ajuster leur comportement au fur et à mesure de la croissance de leur progéniture (Hedd *et al.* 2002, Hipfner *et al.* 2006). Des études basées sur l'échange de poussins d'âges différents entre différents nids, ont montré qu'effectivement les parents ajustaient leur niveau de nourrissage en fonction de l'âge du poussin (Hamer & Hill 1994, Varpe *et al.* 2004). Il semblerait que cet ajustement se fasse en fonction du niveau de sollicitations qui augmente en fonction de l'âge des jeunes (Bertram *et al.* 1996).

De plus, chez certaines espèces, la couvée peut être constituée d'un ou de plusieurs poussins ; l'élevage d'un seul jeune étant susceptible d'infliger un moindre coût aux parents que l'élevage de plusieurs jeunes (Hegner & Wingfield 1987, Sanz & Tinbergen 1999).

Enfin, les caractéristiques individuelles de chaque jeune au sein de la couvée peuvent aussi influer sur l'investissement parental. Ainsi chez les espèces dimorphiques[7], les jeunes mâles et femelles peuvent induire des coûts différents pour les parents si ce dimorphisme préexiste dès le stade "poussin" : par exemple, si les jeunes mâles sont plus lourds et/ou plus grands pendant la phase d'élevage, on peut s'attendre à ce qu'ils occasionnent des coûts plus élevés que les jeunes femelles et qu'alors, les adultes ajustent leur comportement parental en fonction du sexe de leur progéniture (Trivers & Willard 1973, Cameron-McMillan *et al.* 2007).

Qualité de la progéniture et certitude de paternité

Lorsqu'un parent s'investit dans le soin de ses jeunes, il doit confronter son niveau d'investissement et le bénéfice qu'il peut en attendre en termes de fitness. Or les jeunes ne transmettront efficacement les gènes de leurs parents que s'ils sont suffisamment nombreux (chez les espèces où les couvées comprennent plusieurs poussins) et de bonne qualité. Ainsi, un parent est supposé minimiser son investissement dans une couvée de petite taille ou constituée de jeunes trop petits, malades ou faibles (Erikstad *et al.* 1997). La survie de ces jeunes ayant de fortes chances d'être compromise, un parent a tout intérêt à ne pas s'investir dans ce type de couvée au risque de compromettre sa propre fitness. Un exemple est fourni chez la mésange charbonnière *Parus major* : les parents dont la couvée est de petite taille s'investissent moins dans la défense de leur progéniture face aux prédateurs que les parents dont la couvée est de plus grande taille et donc présentant une plus grande valeur en termes de fitness (Curio & Onnebrink 1995).

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[7] **Dimorphisme sexuel** : ensemble des différences morphologiques entre les individus mâles et femelles d'une même espèce.

Le risque de prédation sur la couvée constitue également un facteur susceptible de modifier la qualité de la progéniture : un risque élevé de prédation étant associé à une moindre qualité de couvée (Eggers *et al.* 2006). Ainsi il a été montré chez la paruline verdâtre *Vermivora celata* que les parents diminuent le niveau d'approvisionnement de leurs poussins en réponse à une augmentation de la pression de prédation exercée sur leur nid (Peluc *et al.* 2008). A l'inverse, lorsque la pression de prédation est diminuée, les parents investissent plus dans leur reproduction en augmentant leur taille de couvée et le niveau d'approvisionnement des jeunes (Fontaine *et al.* 2006).

Enfin ce raisonnement peut s'appliquer chez les espèces où les femelles pratiquent des copulations hors couple. Chez ces espèces, contrairement à la femelle pour laquelle l'investissement parental se fait à 100% envers sa propre progéniture, le mâle présente une probabilité variable de ne pas être le père génétique des jeunes dont il s'occupe. Puisque l'investissement parental a pour objectif d'augmenter la propre valeur sélective des parents, le niveau de soins apportés par le mâle à la progéniture covarie positivement avec la certitude que la progéniture est effectivement la sienne (Dixon *et al.* 2002, Kvanermo 2006).

Investissement et condition corporelle du partenaire

Chez les espèces biparentales, l'investissement optimal d'un individu va dépendre non seulement de son propre niveau de dépense parentale mais aussi de celui de son partenaire (Williams 1966, Trivers 1972). La nécessité de rester au nid à jeûner pour prendre soin des poussins alors que le partenaire part à la recherche de nourriture, illustre bien cette interdépendance. Tveraa *et al.* (1997) ont ainsi montré que les pétrels antarctiques *Thalassoica antarctica* étaient capables d'ajuster la durée de leurs voyages alimentaires en fonction de la condition corporelle de leur partenaire : plus la condition corporelle du partenaire est bonne, plus celui-ci est capable de jeûner sur une longue période ce qui permet à l'autre parent de passer plus de temps à s'approvisionner. Cette prise en compte du partenaire ne se limite pas à la condition corporelle mais aussi au comportement de l'autre parent. Ainsi si l'un des deux parents pour une raison particulière, réduit son niveau de soins parentaux, le partenaire se trouve confronté à plusieurs alternatives : (1) compenser complètement ce déficit, (2) le compenser partiellement, (3) garder un niveau d'investissement constant ou encore (4) diminuer lui aussi son investissement dans la reproduction actuelle. Une compensation de la part du partenaire peut entrer en conflit avec ses propres chances de survie : l'existence d'un comportement de compensation dans ce cas signifie que (1) le niveau de dépense supplémentaire occasionnée par cette compensation est insuffisant pour diminuer les chances de survie de l'individu (ex : espèces longévives) ou (2) l'individu est prêt à prendre le risque de compromettre sa survie (ex : espèces à durée de vie courte, individus âgés[8]). Au contraire, l'absence de compensation de la part du partenaire signifie que la prise de risque pour celui-ci est certainement trop grande en termes de survie et de reproduction à venir.

III. 2 – Facteurs intrinsèques au parent

Capacité de reconnaissance et d'intégration des facteurs extrinsèques

Bien évidemment, tous les facteurs extrinsèques énumérés ci-dessus n'ont d'importance que si l'organisme a la capacité de les percevoir (signaux visuels, sonores, olfactifs, tactiles), de les intégrer et de réagir en conséquence (Ball 1993, Nevitt & Bonadonna 2005). On peut s'attendre par exemple à ce que plus les parents consacreront de temps au contact ("à l'écoute") de leur progéniture, plus ils seront capables d'ajuster finement leur comportement à la demande de leur progéniture. Cette dépendance sensorielle a été illustrée notamment par Book (1991) qui a montré qu'un oiseau privé de stimulations tactiles en provenance de sa couvée (par anesthésie locale de la poche incubatrice) abandonne immédiatement son nid.

Durée de vie

En raison d'intérêts divergents entre la reproduction actuelle et les chances de survie du parent, la durée de vie de l'individu va entrer en ligne de compte dans la régulation de l'investissement parental. Ceci va avoir des conséquences importantes sur la plasticité du comportement parental en fonction des contraintes de reproduction. Ainsi chez les espèces à durée de vie courte, on s'attend à ce que les parents ajustent leur comportement en fonction des contraintes de reproduction, quitte à mettre en péril leurs chances de survie (qui *a priori* sont plus faibles que celles des espèces longévives). Au contraire, chez des espèces longévives, les parents sont supposés garder un niveau d'investissement fixe dans la reproduction actuelle même si les contraintes de reproduction augmentent, de façon à maximiser leurs chances de survie et de reproduction future. Ce schéma peut être extrapolé au sein d'une même espèce où les individus

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[8] Cf. paragraphe "Facteurs intrinsèques au parent : *durée de vie*" (p. 21)

présentant une faible probabilité de survie et ayant donc peu de chances de s'engager dans une nouvelle tentative de reproduction (ex : les individus âgés et/ou malades) ont tout intérêt à se "sacrifier" pour leur progéniture (Bonneaud *et al.* 2004, Velando *et al.* 2006). Au contraire, les individus présentant une forte probabilité de survie (ex : les individus jeunes et/ou en bonne santé) ont tout intérêt à "sacrifier" leur progéniture de façon à augmenter leurs chances de survie si les contraintes de reproduction venaient à augmenter.

Sexe du parent

La durée de vie et les chances de survie peuvent être intrinsèquement liées au sexe de l'individu (*e.g.* Dugger *et al.* 2006, Stutchbury *et al.* 2009). Ainsi, on peut s'attendre à ce que des mâles et des femelles d'une même espèce, présentant des durées de vie et des chances de survie différentes, régulent leur investissement parental de manière différente. Pour une même classe d'âge, le sexe ayant le taux de survie le plus important devrait se montrer plus prudent par rapport à l'autre sexe de façon à minimiser le coût de la reproduction.

De plus, mâles et femelles peuvent présenter des caractéristiques physiques et comportementales propres, les spécialisant dans des tâches précises (Prévost 1961, Paredes *et al.* 2008, Požgayová *et al.* 2008, Welcker *et al.* 2009). Le coût de ces tâches peut différer en fonction du sexe. Ainsi, chez certains Alcidés, le mâle nourrit plus longtemps le poussin que la femelle, probablement car contrairement à la femelle, ce surcoût, bénéfique pour le poussin, n'engendre pas de conséquences négatives sur sa fitness (Paredes *et al.* 2006).

Expérience de reproduction

Il a été constaté que les performances de reproduction évoluent avec l'âge et l'expérience de reproduction des individus (Cam & Monnat 2000, Daunt *et al.* 2001, Angelier *et al.* 2007a, Berman *et al.* 2009, Limmer & Becker 2009). Cette observation peut venir du fait (1) que les coûts associés à la reproduction sont différents en fonction de l'âge et de l'expérience (par exemple, plus élevés chez les individus jeunes et inexpérimentés) ou (2) que les individus qui survivent année après année sont aussi ceux qui présentent le meilleur succès reproducteur (Barbraud & Weimerskirch 2005, Sanz-Aguilar *et al.* 2008). Cette deuxième hypothèse suggère que les individus qui survivent tout en ayant le meilleur succès reproducteur sont ceux qui réussissent le mieux à minimiser l'impact négatif de leur investissement parental sur leurs chances de survie et de succès reproducteur à venir (*i.e.* le coût de la reproduction).

Enfin, les membres d'un même couple ayant déjà eu une expérience de reproduction ensemble semblent présenter un meilleur succès reproducteur que des nouveaux couples (Ainley *et al.* 1983, Choudhury 1995, Cézilly & Nager 1996), ce qui sous-entend que les coûts associés à la reproduction diffèrent en fonction de la stabilité ou de l'instabilité du couple.

Condition corporelle et recherche alimentaire

La reproduction demande aux parents d'investir une certaine quantité d'énergie qu'ils vont puiser dans leurs propres réserves. Un exemple mettant en évidence l'importance d'une bonne condition corporelle en vue de se reproduire est fourni par le manchot Adélie *Pygoscelis adeliae* : chez cette espèce, les femelles présentes en début de cycle sur le site de reproduction mais ne se reproduisant pas sont 12% plus légères que celles qui se reproduisent (Vleck & Vleck 2002). La condition corporelle en début de saison de reproduction va donc affecter la décision de se reproduire ou pas. Par ailleurs, un individu présentant une bonne condition corporelle en début de saison de reproduction augmentera ses chances d'obtenir des descendants, eux aussi, en bonne condition corporelle (Chastel *et al.* 1995, Tveraa *et al.* 1998, Vleck & Vleck 2002, O'Dwyer *et al.* 2006). Il a ainsi été montré une forte corrélation entre la masse des poussins et la masse des adultes pendant l'élevage des poussins (Weimerskirch *et al.* 2001, Tveraa & Christensen 2002, Gaston & Hipfner 2006).

Un des facteurs affectant la condition corporelle est la capacité d'un individu à acquérir des ressources alimentaires dans son environnement. Lors de la saison de reproduction, le comportement de recherche alimentaire va dépendre (1) du niveau des ressources disponibles dans l'environnement (Durant *et al.* 2007), (2) de la condition corporelle du parent (Weimerskirch 1998), (3) des besoins de la progéniture (Weimerskirch *et al.* 1996, Harding *et al.* 2002, Gjerdrum 2004) et (4) de la capacité et de l'expérience du parent à acquérir cette nourriture. Ce dernier facteur va lui-même dépendre du sexe (Clarke *et al.* 1998, Peck & Congdon 1998), de l'expérience et de l'âge des individus (Catry *et al.* 2006, Limmer & Becker 2009).

Enfin, le comportement de recherche alimentaire peut être ajusté en fonction de l'avantage accordé par les parents à leur survie ou à la reproduction. Ainsi il a été montré chez de nombreuses espèces d'oiseaux marins que des voyages alimentaires courts permettaient de privilégier les poussins au détriment de la condition corporelle de l'adulte, alors que des voyages longs, imposant aux poussins de jeûner plus longtemps, permettaient aux adultes de restaurer leurs propres réserves (Chaurand & Weimerskirch 1994, Granadeiro *et al.* 1998, Baduini & Hyrenbach 2003, Ropert-Coudert *et al.* 2004). La recherche alimentaire et la redistribution de l'énergie acquise lors des voyages alimentaires apparaissent donc comme les leviers essentiels sur lesquels les parents vont pouvoir jouer pour privilégier leur survie ou leur reproduction.

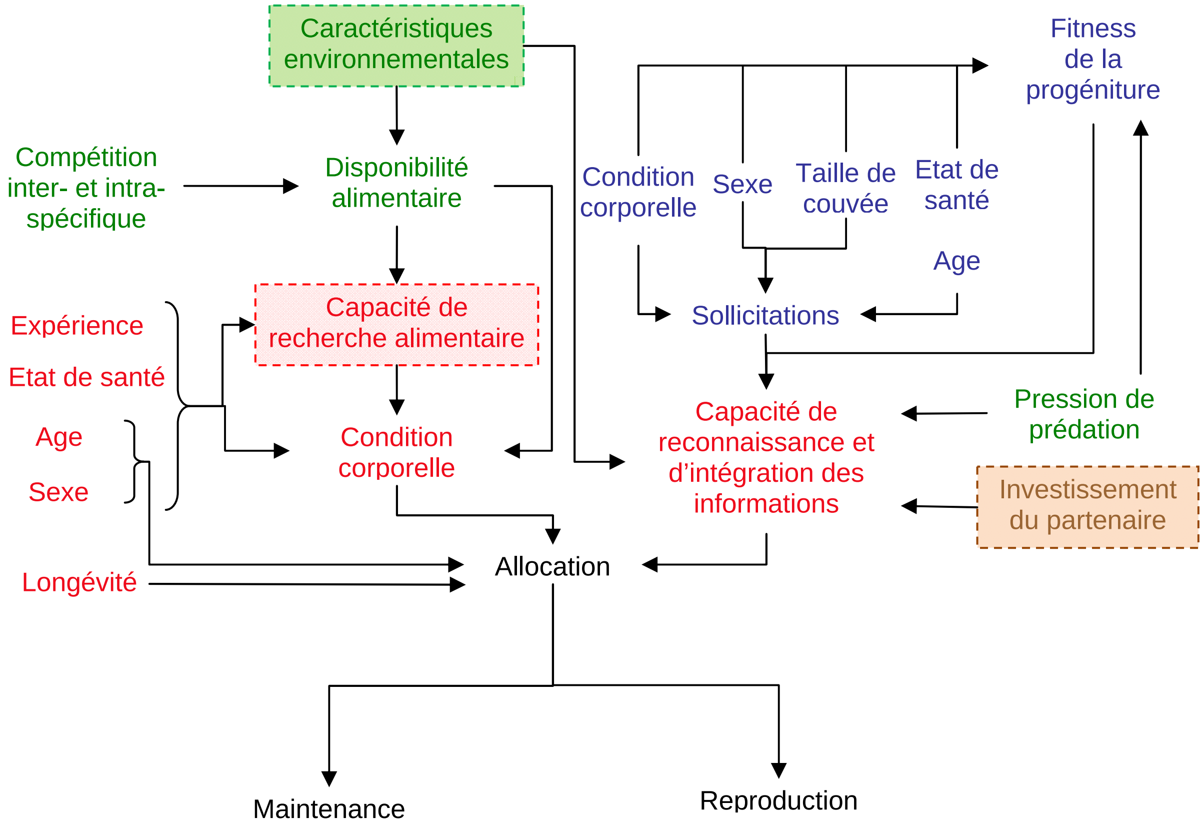

Fig. 1 : Schématisation des différents paramètres susceptibles d'affecter les décisions d'allocation des ressources entre maintenance et reproduction. Rouge : facteurs intrinsèques à l'individu ; vert : facteurs environnementaux ; bleu : facteurs liés à la progéniture ; marron : facteur lié au partenaire (dans le cas d'une espèce où les soins sont biparentaux). Les paramètres encadrés correspondent aux contraintes de reproduction considérées dans ce travail.

IV – Mécanismes physiologiques sous-jacents

IV. 1 – Gestion des réserves corporelles

L'analyse de la condition corporelle et de la gestion des réserves corporelles chez des individus reproducteurs constitue un bon moyen d'étudier l'allocation des ressources entre maintenance et reproduction. La simple mesure de la masse corporelle ou d'un indice de condition corporelle basé sur des critères pondéraux et staturaux, peut donner une idée ponctuelle de la condition de l'animal mais ne permet pas d'évaluer comment celle-ci évolue. Les métabolites, indicateurs des voies anaboliques et cataboliques des lipides et des protéines, peuvent quant à eux être utilisés comme indicateurs de l'état nutritionnel notamment chez les oiseaux (Jenni-Eiermann & Jenni 1998).

Concernant le métabolisme lipidique, la résorption de lipides ainsi que la redistribution des acides gras par le foie vers les autres organes peuvent être estimées par la mesure de la concentration plasmatique en triglycérides. Cette mesure peut ainsi être considérée comme indicatrice de l'état d'engraissement de l'animal (Jenni-Eiermann & Jenni 1994). Le métabolisme protéique quant à lui peut être étudié *via* la mesure de la concentration plasmatique d'acide urique qui, chez les oiseaux, est le produit final du métabolisme azoté et est donc indicateur du catabolisme protéique (Robin *et al.* 1987). Une augmentation de la concentration plasmatique d'acide urique peut donc être révélatrice de la résorption et de la dégradation de protéines d'origine alimentaire ou de l'utilisation des protéines endogènes en cas de déplétion importante des réserves corporelles lors par exemple d'un jeûne prolongé (Cherel *et al.* 1988).

D'autres facteurs peuvent également influer sur les concentrations plasmatiques en métabolites. L'exercice physique se traduit par une augmentation de la concentration plasmatique en acide urique (Jenni-Eiermann & Jenni 1991) et par une diminution de celle en triglycérides (Dewasmes *et al.* 1980). Par ailleurs, la synthèse de l'œuf nécessite la mobilisation et le transfert de ressources protéiques et lipidiques vers l'œuf, d'où une élévation des concentrations plasmatiques en métabolites chez la femelle juste avant la ponte (Vézina & Williams 2003, Kern *et al.* 2005). Enfin, une teneur élevée en lipides ou en protéines dans le bol alimentaire augmente les concentrations plasmatiques de triglycérides et d'acide urique (Gavett & Wakeley 1986).

La lecture des concentrations plasmatiques en métabolites peut donc être utile pour savoir si l'oiseau accumule des réserves ou au contraire entame ses réserves corporelles. Néanmoins, l'interprétation donnée à ces concentrations peut s'avérer délicate puisque leurs variations peuvent dépendre de multiples facteurs.

IV. 2 – Concentrations hormonales

Face aux contraintes associées à la reproduction, l'adoption de telle ou telle décision est sous la dépendance d'une cascade de processus physiologiques. Parmi ces modifications physiologiques, les hormones jouent un rôle prépondérant et apparaissent comme les mécanismes fonctionnels gouvernant les décisions de reproduction (Ricklefs & Wikelski 2002). Pendant la pariade[9], mâles et femelles ont des niveaux d'hormones stéroïdiennes élevés : testostérone chez les mâles et œstrogènes et progestérone chez les femelles (Feder *et al.* 1977, Silver 1978). La testostérone augmente l'agressivité des oiseaux et leur permet de défendre leur territoire ainsi que d'éloigner d'éventuels concurrents (Schoech *et al.* 1998). Chez les femelles, l'action combinée des oestrogènes et de la progestérone stimule la croissance des oviductes et les incitent à copuler (Liley 1976). Après l'obtention et la construction du nid, la pariade, l'accouplement et la ponte, la concentration des hormones stéroïdiennes diminue et reste à des niveaux bas tout au long de l'incubation et de l'élevage des poussins (Vleck *et al.* 1999). Le maintien de niveaux élevés de testostérone nuirait alors à la reproduction en cours en diminuant le niveau des soins parentaux (Silverin 1980, Saino & Møller 1995, Schoech *et al.* 1998). A ce stade, le comportement parental va être soumis à deux hormones principales chez les oiseaux : la prolactine et la corticostérone.

Prolactine

Comme chez la plupart des Vertébrés, la prolactine est impliquée dans l'expression des comportements parentaux chez les oiseaux : elle conditionne l'initiation et le maintien des soins parentaux (Lormée *et al.* 2000, Chastel & Lormée 2002) et stimule le comportement d'incubation (Buntin 1996) et le nourrissage des poussins par les parents (Buntin *et al.* 1991, Duckworth *et al.* 2003). La sécrétion de prolactine augmente parallèlement à la diminution de testostérone. Les niveaux de prolactine restent alors élevés jusqu'à l'éclosion chez les espèces précoces (Dittami 1981) alors qu'ils ne diminuent qu'après l'indépendance thermique chez les espèces tardives (Vleck *et al.* 1999, Lormée *et al.* 2000). Généralement plus élevés chez la femelle, les niveaux de

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[9] **Pariade** : période de formation des couples.

prolactine suivent la même tendance pour les deux parents chez les espèces biparentales (Vleck *et al.* 2002).

Chez les espèces nidifuges, la sécrétion de prolactine dépend de stimuli en provenance des œufs, des poussins ou du partenaire (Buntin 1996). Au contraire, chez les espèces nidicoles, les niveaux de prolactine sont indépendants des stimuli extérieurs (Hector & Goldsmith 1985, Hall 1986) ; ainsi chez les manchots, les longues périodes passées en mer à la recherche de nourriture pendant l'élevage des poussins ne sont pas associées à une diminution des niveaux de cette hormone (Garcia *et al.* 1996, Lormée *et al.* 1999, Vleck *et al.* 2000, Setiawan *et al.* 2006). Par ailleurs, la sécrétion de prolactine peut être diminuée par des conditions environnementales et une disponibilité alimentaire défavorables (Delehanty *et al.* 1997). Il est probable que la diminution de la sécrétion de prolactine lorsque les conditions sont défavorables passe par une diminution concomitante de la condition corporelle. En effet, il a été montré que les niveaux de sécrétion de prolactine étaient positivement corrélés à la masse des oiseaux (Criscuolo *et al.* 2006, O'Dwyer *et al.* 2006). Dans les cas extrêmes, cette réponse peut aboutir potentiellement à l'abandon de la reproduction (Chastel & Lormée 2002, Chastel *et al.* 2005, Groscolas *et al.* 2008). Ainsi, la modulation de la sécrétion de prolactine peut être considérée comme adaptative dans la mesure où elle permet de rediriger l'allocation des ressources vers la reproduction (prolactinémie haute) ou vers la survie (prolactinémie basse).

Par ailleurs, la sécrétion de prolactine semble liée à la sécrétion de corticostérone : une augmentation de corticostérone s'accompagnant d'une diminution durable de la prolactine (Criscuolo *et al.* 2002, Chastel *et al.* 2005, Groscolas *et al.* 2008). Ainsi les niveaux de prolactine doivent être examinés à la lumière des niveaux de corticostérone (Angelier *et al.* 2009a).

Corticostérone

La corticostérone représente le principal glucocorticoïde chez les oiseaux. Dans certaines situations nécessitant la mobilisation des réserves énergétiques, l'axe hypothalamo-hypophyse-glande surrénale est activé et induit la sécrétion de corticostérone (Wingfield & Ramenofsky 1999). Les mesures de la corticostéronémie sont déterminées par le ratio "énergie disponible/demande énergétique" (Landys *et al.* 2006). Ainsi une diminution de la disponibilité alimentaire (Kitaysky *et al.* 1999a, 2007) et/ou des réserves énergétiques de l'organisme (Cherel *et al.* 1988, Groscolas *et al.* 2008) se traduira par une augmentation de la sécrétion de corticostérone. La fonction de cet axe est donc d'adapter l'état physiologique de l'organisme face à des situations énergétiques variables telles que la reproduction, des modifications environnementales ou des situations stressantes (Wingfield *et al.* 1998, Sapolsky 2000). Par exemple, l'augmentation de la demande énergétique occasionnée par la reproduction résultera en l'augmentation de la corticostéronémie (Wingfield *et al.* 1999, Lormée *et al.* 2003, Chastel *et al.* 2005, Landys *et al.* 2006). Néanmoins, des taux trop élevés de corticostérone peuvent induire une diminution de l'effort parental (Silverin *et al.* 1986, Wingfield & Silverin 1986) voire l'abandon total de la reproduction (Groscolas *et al.* 2008), ce qui permet à l'individu de privilégier sa survie aux dépens de la reproduction en cours. Tout comme pour la prolactine, la sécrétion de corticostérone apparaît donc comme un médiateur physiologique important modulant les décisions de reproduction et l'allocation des ressources entre maintenance et reproduction. Ainsi il n'est pas étonnant de constater que chez les oiseaux marins, la corticostéronémie puisse moduler les stratégies de recherche alimentaire en faveur de la maintenance ou de la reproduction (Angelier *et al.* 2007b, 2008).

Du fait de l'interdépendance existant entre corticostérone et prolactine mais aussi parce que la corticostérone et la prolactine peuvent chacune rediriger l'allocation d'énergie vers la reproduction ou la maintenance en fonction des contraintes, ces deux hormones doivent être considérées toutes les deux dans le cadre d'études portant sur l'investissement parental (Angelier *et al.* 2009b)

IV. 2 – Stress oxydant et dynamique des télomères

Un autre moyen d'étudier comment un animal reproducteur alloue ses ressources entre maintenance et reproduction consiste à examiner si celui-ci est capable de se défendre physiologiquement contre les effets négatifs de la reproduction. Le stress oxydant représente une bonne illustration de cette capacité à se défendre et donc à privilégier sa maintenance.

Le métabolisme aérobie aboutit à la génération de radicaux chimiques dérivés de l'oxygène (Reactive Oxydative Species ou ROS) au sein de la mitochondrie. Ces ROS peuvent réagir avec d'autres composés biologiques et induire des dommages sur les lipides, les protéines ou les acides nucléiques, ce qui aboutit à la génération de métabolites dérivés de l'oxygène (Reactive Oxydative Metabolites ou ROM). Pour contrer l'action des ROS, l'organisme peut se défendre grâce à des composés antioxydants exogènes (*e.g.* caroténoïdes, vitamines E) et endogènes (enzymes, *e.g.* superoxyde dismutase, glutathion peroxydase) transformant les ROS en espèces moins réactives (Vleck *et al.* 2007, Cohen & McGraw 2009). Le stress oxydant se définit comme l'état de déséquilibre entre les ROS et la capacité antioxydante de l'organisme (Finkel & Holbrook 2000). De récentes études ont avancé l'idée que le stress oxydant pouvait servir de médiateur dans le coût de la reproduction. Par exemple, chez le diamant mandarin *Taeniopygia guttata,* il a été montré qu'une augmentation de l'effort de reproduction induisait une diminution de la capacité antioxydante des parents (Alonso-Alvarez *et al.* 2004, Wiersma *et al.* 2004). Par ailleurs, chez le martinet alpin *Apus melba*, la résistance au stress oxydant est reliée à la fécondité (chez les femelles) et à la survie (chez les mâles ; Bize *et al.* 2008). Cela suggère que le statut oxydant de l'animal pourrait être un des mécanismes physiologiques sous-tendant le compromis entre reproduction et maintenance.

Le lien entre stress oxydant et maintenance pourrait avoir une étape supplémentaire : l'impact négatif du stress oxydant sur la longueur des télomères. Les télomères sont des séquences nucléiques non-codantes qui chapotent les extrémités des chromosomes des cellules eucaryotes et stabilisent le génome. Ils se raccourcissent classiquement à chaque division cellulaire du fait du problème de réplication de l'extrémité 5'-3'. Une fois que la longueur des télomères atteint un certain seuil, la cellule rentre en apoptose[10] (Blackburn 2000). Par conséquent, la longueur des télomères donne un indice de l'âge biologique de l'individu (Monaghan & Haussmann 2006). Le stress oxydant, en conduisant à une accélération du rétrécissement des télomères (von Zglinicki 2002, Richter & Von Zglinicki 2007), pourrait ainsi accentuer le phénomène de sénescence[11]. En effet, la dynamique des télomères a été récemment reliée au taux de survie chez les martinets alpins (Bize *et al.* 2009) et les choucas des tours *Corvus monedula* (Salomons *et al.* 2009) et pourrait donc être le lien fonctionnel entre l'intensité du stress subi par l'animal au cours d'une saison de reproduction et la réduction de ses chances de survie.

V – Modèle d'étude et objectifs

V .1 – Modèle d'étude

Notre étude a porté sur une espèce longévive et biparentale : le manchot Adélie *Pygoscelis adeliae*. L'ensemble des études publiées sur cette espèce constitue une base bibliographique

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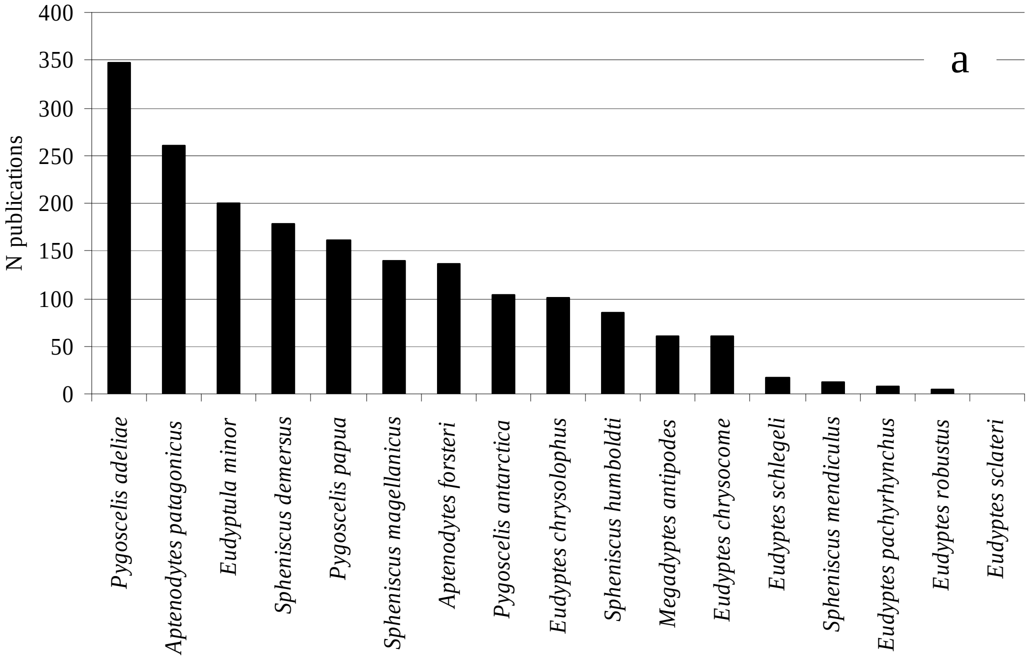
[10] **Apoptose** : mort cellulaire programmée.

[11] **Sénescence** : à l'échelle de l'organisme, diminution avec l'âge des chances de survie et du succès reproducteur.

consistante. Ainsi parmi les différentes espèces de manchots et les différents oiseaux antarctiques, le manchot Adélie est de loin l'espèce la plus étudiée (Fig. 2).



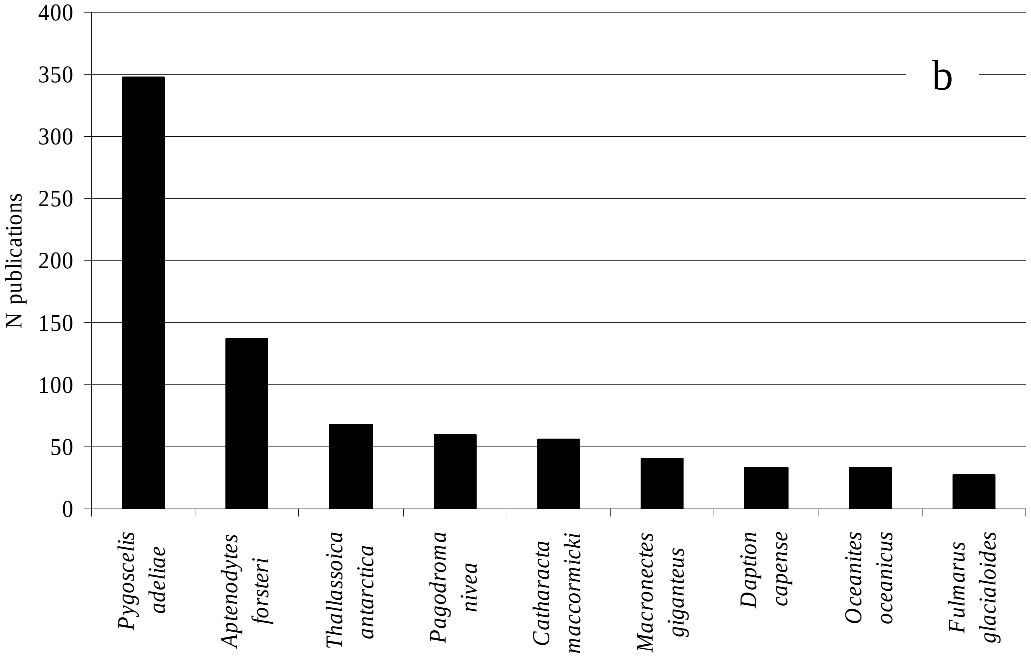


Fig. 2 : Nombre d'articles publiés sur les (ou faisant référence aux) manchots (a) et sur les oiseaux antarctiques (b). Recherche effectuée en août 2009 sur EndNote en se connectant sur "ISI web of knowledge" et en recherchant le nom latin de chaque espèce (entre guillemets) dans la section "Title/Keywords/Abstract".

La plupart des études sur le manchot Adélie ont porté sur son écologie alimentaire. Ces études se sont principalement focalisées sur la quantité et la qualité des proies consommées (*e.g.* Kent *et al.* 1998, Wienecke *et al.* 2000), la durée de leurs voyages alimentaires (*e.g.* Watanuki *et al.* 1993, Clarke *et al.* 2002), leur distribution spatiale (*e.g.* Clarke *et al.* 2003) et leur comportement de plongée. Ces deux derniers paramètres ont été mesurés grâce à des transmetteurs (ex : balises Argos) ou des enregistreurs placés sur l'animal et capables de mesurer entre autres la profondeur (*e.g.* Ropert-Coudert *et al.* 2002) ou les mouvements du manchot (*e.g.* Yoda *et al.* 2001). Le succès reproducteur et la dynamique de population ont également été étudiés et reliés aux changements environnementaux (principalement les conditions de glace ; Kato & Ropert-Coudert 2006, Jenouvrier *et al.* 2006, Emmerson *et al.* 2008), au dérangement engendré par la présence humaine (Giese 1996, Carlini *et al.* 2007) ou encore à l'utilisation de bagues d'identification (Dugger *et al.* 2006). Des études portant sur l'énergétique du comportement de recherche alimentaire (*e.g.* Chappell *et al.* 1993a, b) ou sur l'évolution des concentrations hormonales tout au long du cycle (*e.g.* Vleck *et al.* 1999) ont également été conduites.

Au final, deux grands types d'études se détachent : des études portant sur l'individu (écologie alimentaire, physiologie) et des études se situant à l'échelle de la population. Or la population évoluera en fonction de la capacité des individus la constituant à survivre et à produire des descendants féconds. Ainsi l'évolution d'une population est liée à la capacité des individus à investir dans la reproduction et aux conséquences de la reproduction sur leur capacité de survie. Or, comme chez tous les oiseaux marins, le succès reproducteur chez le manchot Adélie ne dépend pas d'un seul individu mais des deux parents. Paradoxalement très peu d'études se sont intéressées à la régulation de l'investissement parental à l'échelle du couple chez cette espèce. Par conséquent, les interactions comportementales entre les parents et leurs implications sur la physiologie des individus et leur succès reproducteur restent méconnues.

Par ailleurs, l'étude des mécanismes physiologiques susceptibles d'affecter les décisions de reproduction a à peine été abordée chez le manchot Adélie (Vleck & Vleck 2002, Angelier *et al.* 2008).

V. 2 – Objectifs

L’objectif général de ce travail de thèse était de tester le compromis entre reproduction et maintenance chez les deux membres du couple de manchot Adélie. Un moyen d'étudier ce compromis chez une espèce biparentale consiste à soumettre le couple à différentes contraintes de reproduction[12] portant sur l'un des membres du couple ou sur les deux à la fois.

La première contrainte, **expérimentale**, a consisté à handicaper un des parents au sein de couples de manchots Adélie de façon à diminuer sa capacité de recherche alimentaire tout au long de la saison de reproduction (Fig. 1).

La deuxième contrainte, **environnementale**, a consisté à suivre un même groupe de manchots Adélie dans des conditions environnementales différentes (en l'occurrence, les conditions de glace de mer) susceptibles de modifier la disponibilité alimentaire (Fig. 1).

De la première contrainte expérimentale découle une troisième contrainte : **l’investissement du partenaire**. En effet, puisqu’il était vraisemblable que le niveau de soins apportés au(x) poussin(s) par l’individu handicapé soit plus faible que celui d’un individu contrôle, il était également possible que cela constitue une contrainte pour le partenaire de l'individu handicapé (Fig. 1).

Dans les deux cas de figure, nous avons évalué les réponses comportementales à terre et en mer des deux parents, ainsi que les effets sur leur progéniture en termes de succès reproducteur et de masse corporelle des poussins. Les concentrations plasmatiques de corticostérone et de prolactine ont été mesurées de façon à mieux comprendre les mécanismes physiologiques sous-tendant les décisions de reproduction face à ces deux contraintes. Les conséquences à long terme telles que la survie et la fécondité des parents ont également été étudiées et mises en relation avec les niveaux de stress oxydant et la dynamique des télomères des oiseaux suivis.

Les objectifs de chaque article sont détaillés ci-dessous :

- **Article 1** (contrainte expérimentale) : Evaluation de la réponse comportementale des individus handicapés et de leurs partenaires et effets à long terme sur leur survie et leur fécondité. Etude des conséquences sur les poussins en termes de succès reproducteur, de masse corporelle et de comportement envers les parents.

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[12] **Contrainte de reproduction** : ici considérée comme tout paramètre susceptible de moduler l'investissement parental.

- **Article 2** (contrainte expérimentale) : Identification des phases critiques du cycle reproducteur susceptibles de modifier le succès reproducteur des couples handicapés.
- **Article 3** (contrainte environnementale) : Evaluation de la réponse comportementale et physiologique d'individus reproducteurs et étude des conséquences sur les poussins en termes de succès reproducteur et de masse corporelle.
- **Article 4** (contrainte expérimentale et environnementale) : Etude de la capacité de recherche alimentaire *via* le comportement de plongée.
- **Article 5** (contrainte expérimentale) : Etudes de paramètres physiologiques et alimentaires chez les individus handicapés et leurs partenaires.
- **Article 6** (contraintes expérimentale et environnementale) : Mesure des concentrations de corticostérone et de prolactine.
- **Article 7** (contrainte expérimentale) : Mesure du stress oxydant et de la dynamique des télomères chez des manchots handicapés et contrôles
- **Article 8** (contrainte environnementale) : Mise en relation du statut oxydant et des stratégies de recherche alimentaire.

Le sexe du poussin a également été considéré lors de ce travail de thèse comme étant une contrainte potentielle pour les parents en considérant que les poussins mâles et femelles avaient des besoins différents pendant leur élevage. Du fait que l'étude de cette contrainte a été, pour l'instant, moins approfondie que les deux autres, nous ne l'avons pas inclue dans ce manuscrit. Un article (Article 9) à ce sujet a tout de même été ajouté en annexe.

2

METHODOLOGIE

Méthodologie

I – Site d'étude

Lors de ces trois années de thèse, j'ai pu effectuer deux campagnes d'été (2 x 3,5 mois en 2006-07 et 2007-08) sur la station scientifique française Dumont d'Urville (66°40'S ; 140°01'E) en Terre Adélie. Dumont d'Urville se trouve sur l'Ile des Pétrels qui représente l'île la plus grande de l'Archipel de Pointe Géologie, en bordure du continent antarctique (Fig. 3). L'Ile des Pétrels compte environ un tiers des 35000 couples de manchots Adélie présents sur l'archipel.

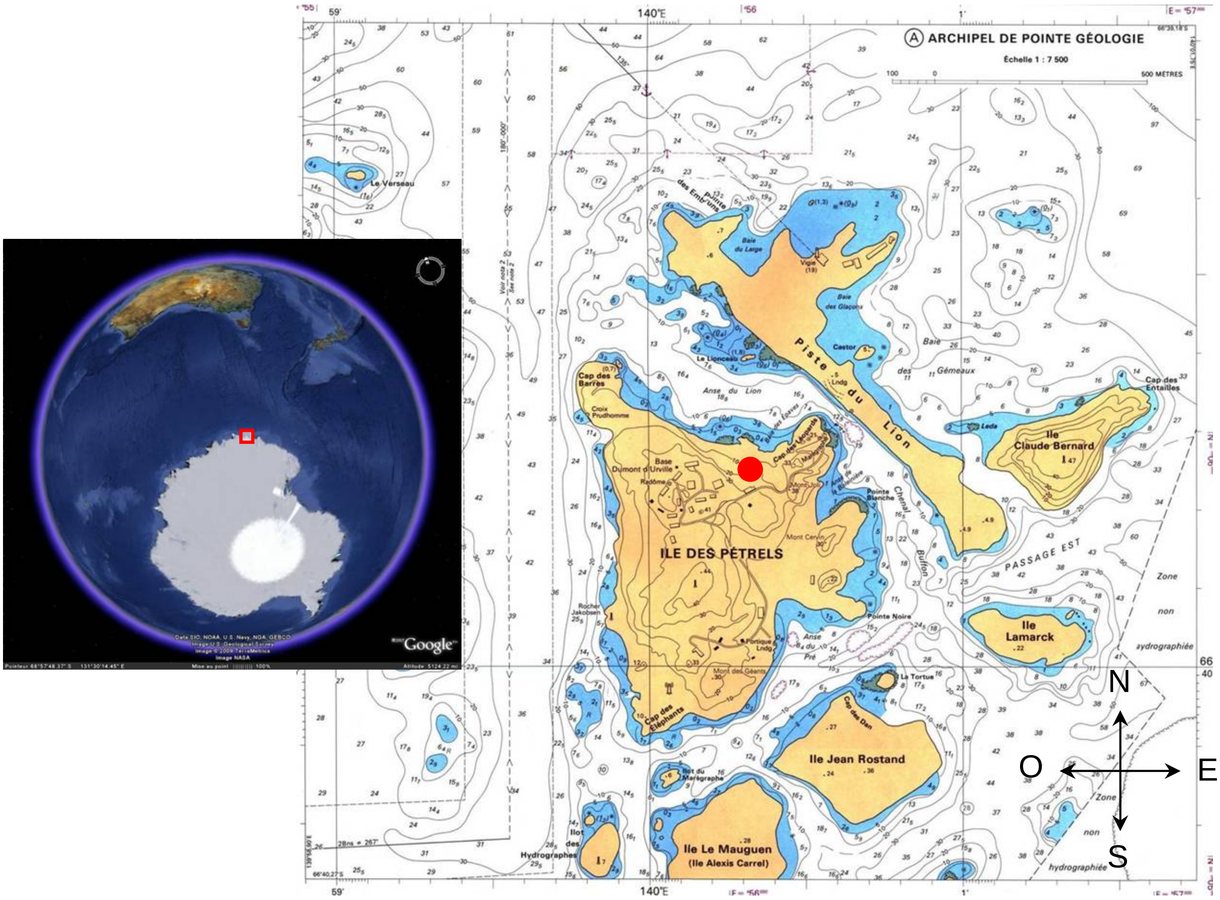

Fig. 3 : Localisation de l'Archipel de Pointe Géologie (carré rouge) en bordure du continent Antarctique et localisation de la colonie d'étude (rond rouge) sur l'Ile des Pétrels.

Le choix de la colonie s'est porté sur un sous-groupe constitué de plus de 200 couples et situé à proximité du laboratoire de façon à faciliter les manipulations et les observations (Fig. 4).

Fig. 4 : Vue aérienne de la colonie d'étude (centre de la photographie) et du laboratoire de biologie à Dumont d'Urville.

II – Généralités sur la biologie du manchot Adélie

Le manchot Adélie fait partie avec le manchot empereur des deux espèces de manchot se reproduisant uniquement en bordure du continent Antarctique. Il s'agit d'une espèce longévive[13] et monogame[14]. La population de l'Archipel de Pointe Géologie est en constante augmentation au moins depuis le début des années 1980 avec un taux d'augmentation de 1,77% chaque année (Jenouvrier *et al.* 2006). La saison de reproduction a lieu annuellement d'octobre à mars, pendant l'été austral.

Le cycle du manchot Adélie se décompose en cinq phases : la pariade, l'incubation, le stade de garde, le stade de crèche et la mue (Fig. 5).

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[13] Age maximum estimé à 20 ans (Ainley 2002).

[14] **Espèce monogame** : espèce chez qui les individus n'ont qu'un seul partenaire par saison de reproduction.

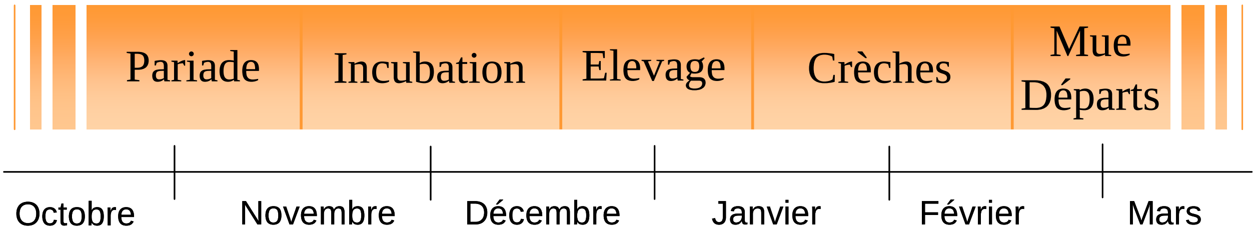


Fig. 5 : Cycle de reproduction du manchot Adélie.

- la **pariade** : les mâles arrivent en premier sur le nid de l'année précédente. Les femelles arrivent en moyenne un jour plus tard et choisissent leur partenaire (Davis & Speirs 1990).
- L'**incubation** : après la ponte d'un ou deux œufs, la femelle part se nourrir en mer pour un voyage de 10-12 jours. Le mâle se voit donc confier le premier "shift" d'incubation pour une durée correspondante. Après ce premier voyage en mer, les femelles reviennent au nid et assument le deuxième "shift" d'incubation pendant que le mâle part se nourrir en mer pour une durée de 10-12 jours. Mâles et femelles alternent ensuite un ou deux voyages en mer de quelques jours jusqu'à la fin de l'incubation, à l'éclosion des œufs, 34 jours en moyenne après la ponte.
- Le **stade de garde** : l'élevage des poussins dure en moyenne trois semaines et se caractérise par la présence obligatoire d'un parent au nid alors que l'autre est en mer à la recherche de nourriture. La présence d'un parent au nid est rendue obligatoire du fait de la thermodépendance des poussins (12-15 premiers jours) et de l'incapacité des poussins à se défendre contre des prédateurs potentiels (Skua antarctique *Catharacta maccormicki*). Du fait de copulations hors-couple, on estime qu'environ 10% des poussins ne sont pas élevés par leur propre père (Pilastro *et al.* 2001).
- Le **stade de crèche** (Fig. 6) : une fois que les poussins ont acquis leur indépendance thermique et qu'ils sont aptes à se défendre seuls contre les prédateurs éventuels, les parents, libres de partir en mer simultanément, les laissent seuls sur la colonie. Les poussins alors mobiles se regroupent les uns contre les autres lorsque les conditions climatiques se dégradent et forment des "crèches". Au cours de cette période de deux-trois semaines, les parents reviennent sporadiquement sur la colonie pour nourrir leur(s) poussin(s). Ils reviendront de moins en moins jusqu'à ne plus revenir sur la colonie pour nourrir leurs poussins.

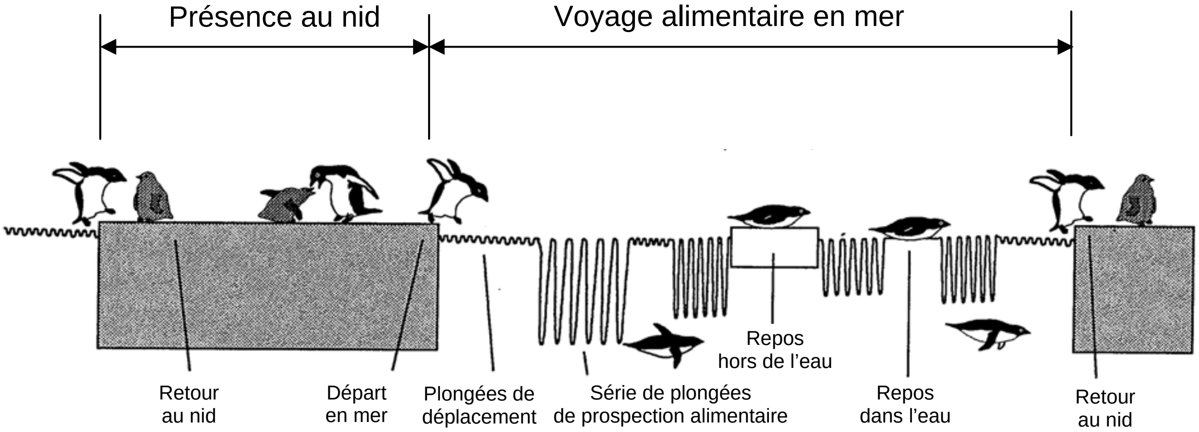


Fig. 6 : Schématisation des différentes périodes lors de l'élevage du poussin chez le manchot Adélie (d'après Chappell et al. *1993a).*

- La **mue** : une fois le stade de crèche terminé, les parents partent se nourrir en mer afin d'emmagasiner suffisamment d'énergie pour la mue à venir. Les poussins perdent alors leur duvet qui est remplacé par des plumes leur permettant de partir en mer. Les adultes reviennent un peu plus tard à terre pour un nouveau jeûne d'environ deux semaines où toutes leurs plumes seront renouvelées (Ainley 2002). Ils repartent alors pour leur migration hivernale.

Chez le manchot Adélie, l'activité de recherche alimentaire est l'activité la plus coûteuse pendant le cycle de reproduction. Elle conduit à un doublement du taux métabolique journalier des adultes reproducteurs alors même que cette activité ne représente qu'un peu moins du tiers du budget temps lors de l'incubation, du stade de garde et du stade de crèche (Chappell *et al.* 1993a, b ; Fig. 7). Le coût associé à l'activité de nage en elle-même représente quatre à six fois le taux métabolique de repos chez le manchot Adélie (Chappell *et al.* 1993a)

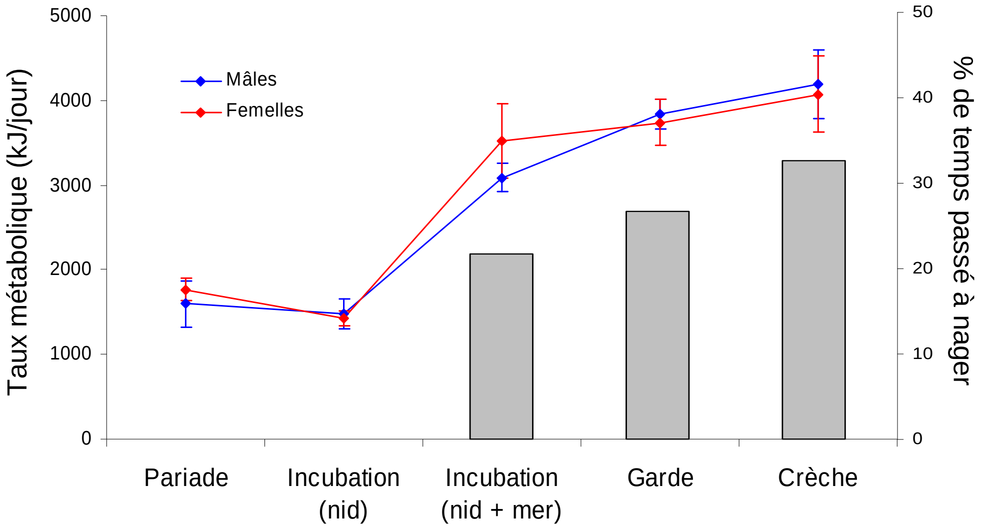


***Fig.* 7** *: Taux métaboliques (courbes) et pourcentage de temps passé à nager (histogrammes) tout au long du cycle reproducteur chez des manchots Adélie mâles et femelles (d'après Chappell* et al. *1993a, b).*

En fonction de la localisation des colonies, le régime alimentaire des manchots Adélie peut varier. Ils peuvent se nourrir :

- de krill exclusivement : krill antarctique *Euphausia superba* principalement (Coria *et al.* 1995, Trivelpiece *et al.* 2003, Lynnes *et al.* 2004), mais aussi krill des glaces *E. crystallorophias* (Emison *et al.* 1968, Ainley *et al.* 2003),
- d'un mélange de poisson (calandre antarctique *Pleuragramma antarcticum*) et de krill dans des proportions diverses (Watanuki *et al.* 1997, Clarke *et al.* 1998, Olmastroni *et al.* 2004). C'est ce dernier cas qui est rencontré à Dumont d'Urville (Ridoux & Offredo 1989, Ropert-Coudert *et al.* 2002).

La densité énergétique ainsi que les contenus lipidiques et protéiques d'*E. superba* et de *P. antarcticum*, les deux proies principales des manchots Adélie de Terre Adélie, sont présentés en annexe (Tableau 11).

III – Procédure

La procédure générale a été la même lors des deux campagnes d'été (hormis le handicap ayant eu lieu uniquement en 2006-07; Fig. 12). Ceci nous a permis de suivre de manière identique les mêmes individus (et leurs nouveaux partenaires, s'ils en avaient changé en 2007-08) pendant deux saisons de reproduction consécutives.

III. 1 – Procédure générale

Quelques jours avant la ponte, courant novembre 2006, 46 couples de manchots ont été aléatoirement sélectionnés parmi les 200 couples de la colonie. Une prise de sang a tout d'abord été effectuée sur seringue héparinée, dans les cinq minutes suivant l'approche vers le nid. Chaque manchot a ensuite été pesé (balance électronique, Ohaus, ± 2g) et la longueur de l'aileron, du culmen ainsi que le tour de thorax ont été mesurés (± 1 mm). Parmi les 92 manchots, 30 ont été handicapés en 2006-07 (Cf. ci-dessous). Avant d'être relâchés à proximité de leur nid, chaque manchot a été identifié par une marque de teinture brune (Nyanzol ®) peinte sur le thorax et par un transpondeur (31,2 x 3,8 mm ; 0,8 g ; Texas Instruments TIRIS) implanté en position sous-cutanée, dans la peau lâche entre la queue et la patte gauche. Aucun effet délétère lié au transpondage n'a pu être détecté par la suite.

Afin de minimiser le dérangement sur un même nid, le partenaire a subi le même traitement (hormis le handicap) deux jours plus tard.

Pendant les phases d'incubation et d'élevage, les couples ont été suivis à distance, à la jumelle, au pire toutes les deux heures et au mieux en continu. Cela nous a permis de noter les dates de ponte, le nombre d'œufs pondus, les départs en mer et les retours de mer (et donc la durée des voyages alimentaires) ainsi que le succès reproducteur.

Les manchots ont été sexés par une combinaison de paramètres incluant l'inspection cloacale avant la ponte (Fig. 8), l'observation des comportements de copulations et l'alternance des "shifts" d'incubation. L'inspection cloacale en vue de déterminer le sexe a été mise au point pendant la manipulation des oiseaux et la détermination du sexe à partir de ce paramètre anatomique a été entièrement confirmée par les paramètres comportementaux cités ci-dessus et par la lipémie des échantillons sanguins : celle-ci étant bien plus élevée chez les femelles avant la ponte du fait de la mobilisation des réserves pour la synthèse de l'œuf (Cf. Article 3).

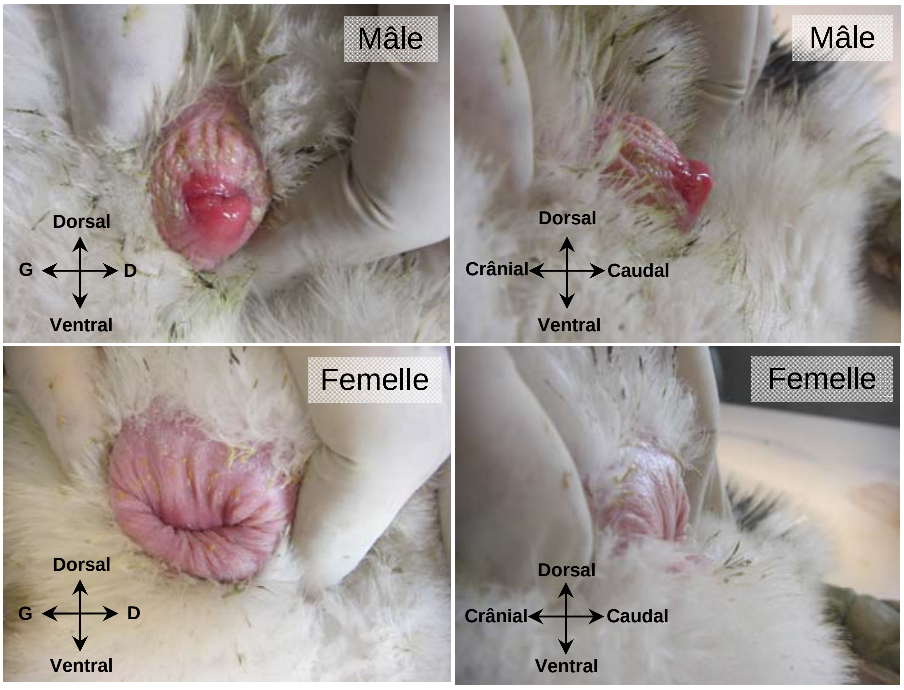


Fig. 8 : Inspection cloacale de manchots Adélie mâles (haut) et femelles (bas) quelques jours avant la ponte.

Quarante à quarante-cinq jours après la ponte, les manchots expérimentaux ont été à nouveau capturés afin de prélever du sang dans les mêmes conditions que précédemment et de les peser. La présence du transpondeur a alors été vérifiée à ce stade et 100% des manchots se sont avérés avoir gardé leur transpondeur. Tout comme lors de la première prise de sang, les échantillons sanguins ont été centrifugés et le plasma ainsi que les globules rouges ont été congelés (-20°C) avant d'être rapatriés en France où les dosages ont eu lieu (Cf. Articles 3, 5, 6, 7 et 8 pour plus de précisions sur les différents dosages).

Quelques jours avant le stade de crèche, les poussins encore inféodés à leur nid ont été légèrement marqués à l'aide de peinture en spray (Raidex, Raidex GmbH) de façon à pouvoir les retrouver et les peser une fois laissés seuls pour la première fois par leurs parents (transition "stade de garde/stade de crèche"; Fig. 12).

Depuis 2007-08, le taux de retour des manchots étudiés en 2006-07 est noté grâce à leur transpondeur. En 2007-08, ceux-ci (et leurs nouveaux partenaires) ont été suivis comme l'année précédente mais aucun manchot n'a été handicapé. Ceci nous à permis de connaître les conséquences à long terme du handicap (Article 1) et d'étudier les manchots contrôles dans deux conditions environnementales différentes (Article 3).

III. 2 – Procédure expérimentale : le handicap

Parmi les méthodes de handicap qui ont été utilisées chez les oiseaux (Hinde 2006), nous en avons choisi une qui diminue les propriétés hydrodynamiques des manchots en mer. Lorsqu'un animal plongeur est équipé d'enregistreurs externes, trois paramètres principaux sont à prendre en considération (Bannasch *et al.* 1994) : (1) la forme, (2) la position, (3) la section frontale de l'équipement relative à la section frontale de l'animal. Afin de minimiser les effets délétères consécutifs à l'équipement (augmentation de la durée des voyages alimentaires, perte de masse, diminution du succès reproducteur...), il est recommandé d'utiliser des appareils de forme hydrodynamique, attachés en bas du dos de l'animal et dont la section frontale correspond à moins de 1% de la section frontale de l'animal. Ici, le but étant d'handicaper les manchots, nous sommes allés à l'encontre de ces recommandations : nous avons attaché au milieu du dos des manchots des prismes de plexiglas (25 x 35 x 60 mm, 60 g) dont la section frontale correspondait à 3-4% de celle des manchots. Ces prismes de plexiglas ont été accrochés aux plumes du dos avec du mastic, de la colle cyanoacrylate, du scotch marin (Tesa ®) et des colliers de serrage (Fig. 9).

Fig. 9 : Méthode d'attachement du handicap sur les plumes du dos (gauche) et manchot Adélie équipé d'un handicap (droite).

Même si la taille des appareils enregistreurs ("loggers") ou émetteurs n'a cessé de diminuer depuis une vingtaine d'années (Fig. 10 ; r_s=-0.63, P=0.005), la taille du handicap utilisé pour notre étude se trouve dans la gamme de taille des loggers utilisés depuis le début des années 1990 chez cette espèce (Fig. 10).

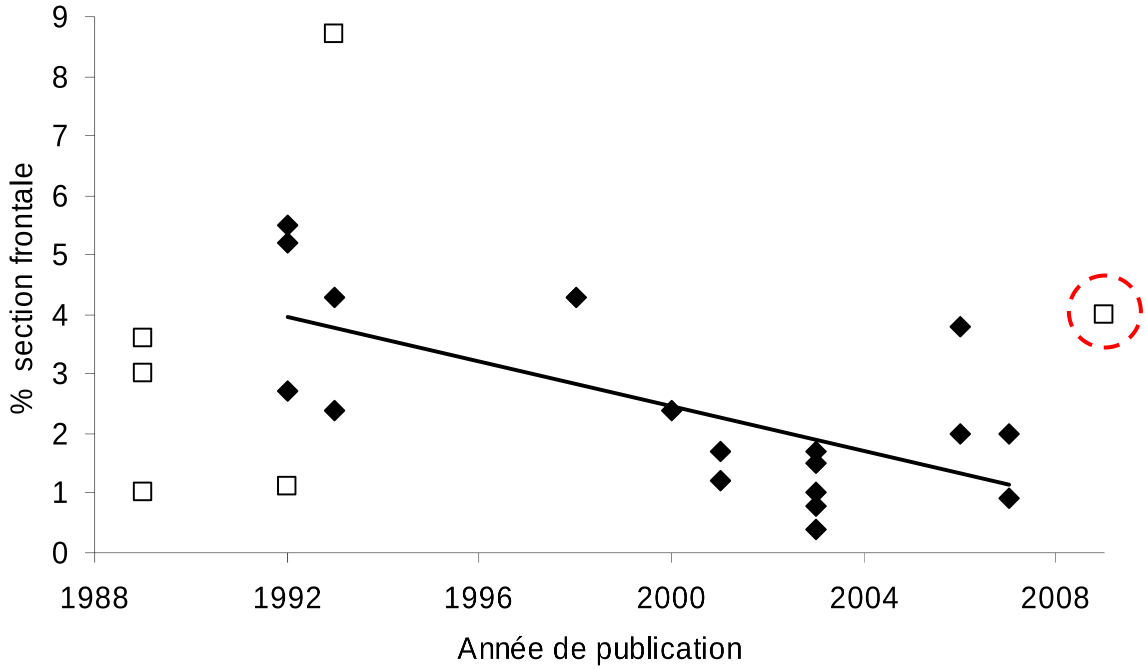


Fig. 10 : Section frontale des appareils ayant servis à équiper des manchots Adélie lors du cycle de reproduction depuis le début des années 1990 (Wilson et al. *1989, Culik & Wilson 1992, Davis & Miller 1992, Watanuki* et al. *1992, Miller & Davis 1993, Chappel* et al. *1993a, Clarke* et al. *1998, Rodary* et al. *2000, Ballard* et al. *2001, Ropert-Coudert* et al. *2001, Kato* et al. *2003, Watanuki* et al. *2003, Clarke* et al. *2006, Ropert-Coudert* et al. *2007, Article 1). La section frontale est exprimée en pourcentage de la section frontale des manchots, celle-ci ayant été calculée à partir des mesures de périmètre thoracique obtenues dans notre étude et en considérant que ce périmètre thoracique était circulaire. Losanges noirs : enregistreurs réels, carrés blancs : fac-similés d'enregistreurs (le carré blanc entouré d'un cercle rouge correspond à notre étude).*

Le paramètre le plus souvent pris en considération dans les études ayant examiné les effets de l'équipement chez le manchot Adélie est la durée des voyages alimentaires (Tableau 1). La section frontale moyenne des enregistreurs ayant conduit à une augmentation de la durée des voyages alimentaires est de 4,3 ± 0,8% (moyenne ± SE) alors que celle des enregistreurs n'ayant pas modifié ce paramètre est de 1,6 ± 0,2% (moyenne ± SE, en considérant la section frontale de l'enregistreur le plus grand dans le cas d'études ayant utilisé différentes tailles d'enregistreurs).

Tableau 1 : Récapitulatif des études ayant examiné l'effet de l'équipement chez des manchots Adélie lors du cycle de reproduction.(+ : augmentation du paramètre, – : diminution du paramètre, = : paramètre inchangé)

	Masse du logger (g)	% Section frontale*	Nombre de voyages	Durée des voyages alimentaires	Masse des adultes	Fréquence de nourrissage	Succès reproducteur	Remarques
Wilson *et al.* 1989	6 - 35 - 48	1 - 3,0 - 3,6	≥ 1	+				
Culik & Wilson 1992	35	1,1		+				
Davis & Miller 1992	160	5,5	1	+	–			
Watanuki *et al.* 1992	80 - 150	2,7 - 5,2		+		–	–	Effets si harnais
Miller & Davis 1993	de 110 à 180	de 4,3 à 8,7	1	+	–			
Chappell *et al.* 1993	45	2,4	1	=				
Clarke *et al.* 1998	90 - 160	4,3		+			–	Effets si équipement avant l'éclosion
Rodary *et al.* 2000	50	2,4		+				Effets pendant le stade de crèche
Ballard *et al.* 2001	15 - 25	1,2	>2	=				
Ropert-Coudert *et al.* 2001	50	1,7		=				
Kato *et al.* 2003	26 - 36 - 66	0.8 - 1,5 -1,7	1	=				
Watanuki *et al.* 2003	9.5 - 14	0,4 - 1	7	=	=			
Clarke *et al.* 2006	90 - 120	2 - 3,8	de 1 à 26	=/+				
Ropert-Coudert *et al.* 2007	17 - 50	0,9 - 2	1	=				

* rapport entre la section frontale de l'instrument et la section frontale du manchot Adélie

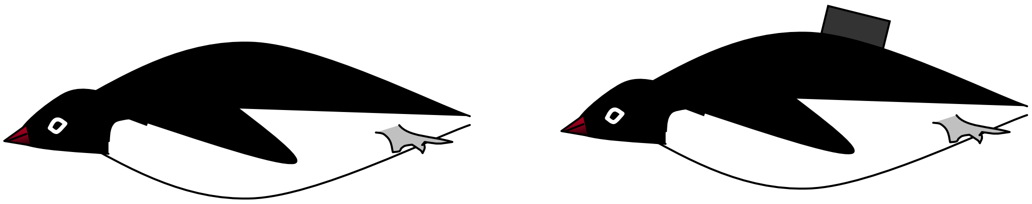
Bannasch *et al.* (1994) ont montré qu'un instrument de taille similaire au nôtre était susceptible de doubler la résistance à l'avancement ("drag") d'un manchot. De plus, Culik & Wilson (1991) rapportent que le coût de transport de manchots Adélie équipés avec un instrument dont la section frontale ne représentait que 2% de celle du manchot, voyaient leur coût de transport augmenter de 25%. Il était donc vraisemblable que les handicaps utilisés dans notre étude augmentent au moins le coût de transport des manchots handicapés et la durée de leurs voyages alimentaires et donc diminuent la fréquence d'approvisionnement des poussins.

III. 3 – Comportement d’incubation

Afin de mettre en évidence d’éventuelles altérations du comportement d’incubation chez des manchots handicapés, le taux d’éclosion a été comparé entre des couples handicapés et des couples contrôles et le comportement d’incubation a été suivi chez 18 manchots mâles (9 handicapés, 9 contrôles) à l’aide d’œufs artificiels fabriqués au DEPE et permettant de mesurer la température d’incubation et le taux de rotation (Fig. 12, Article 2).

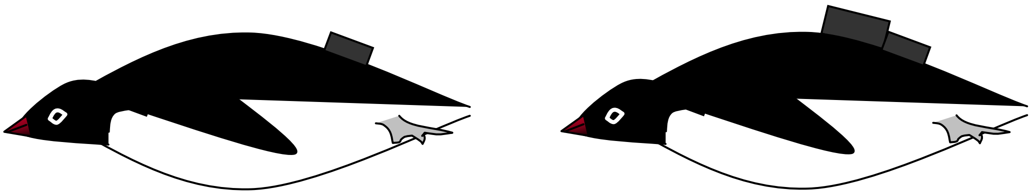
III. 4 – Comportement de recherche alimentaire

Afin de comparer le comportement de recherche alimentaire entre des manchots contrôles et des manchots handicapés, un autre lot de 14 manchots mâles a été équipé d'enregistreurs de plongées (mk9, Wildlife Computers ; 65 x 18 x18 mm, 30 g). La moitié d'entre eux a été équipée d'un mk9 uniquement alors que l'autre moitié a été équipée d'un prisme de plexiglas à l'arrière duquel était attaché un mk9 (Fig. 11 et 12). La technique d'attachement correspond à celle décrite précédemment (Fig. 9) ; les prismes de plexiglas se trouvant au milieu du dos et les mk9 en position plus caudale (Fig. 11). Cette étude portant sur la recherche alimentaire a été menée sur les deux années et a donc pu permettre, en plus de comparer le comportement de plongée d'individus handicapés à celui d'individus contrôles, de comparer le comportement de plongée en fonction des contraintes environnementales caractérisant chaque année (Article 4).



Manchot contrôle ou partenaire

Manchot handicapé



Manchot contrôle (mk9)

Manchot handicapé (mk9)

Fig. 11 : Schématisation des différents lots de manchots suivis lors de ce travail de thèse. Les manchots contrôles ne portent aucun équipement. Les manchots handicapés sont équipés de prisme de plexiglas et ont pour partenaire des manchots non-équipés. Dans le cadre de l'étude portant sur la recherche alimentaire, les manchots contrôles portent un enregistreur de plongée (mk9) et les manchots handicapés portent un enregistreur de plongée et un prisme de plexiglas.

III. 5 – Etude comportementale portant sur les poussins

Pendant l'élevage des poussins en 2006-07, 39 retours au nid après un voyage alimentaire ont été filmés à distance pendant 90 minutes afin de noter le nombre et la durée des sollicitations des poussins vers les adultes et le nombre et la durée des nourrissages des adultes vers les poussins.

Le détail de l'analyse des différentes données est fourni dans la section "Matériel et méthodes" de chacun des articles présentés dans ce mémoire.

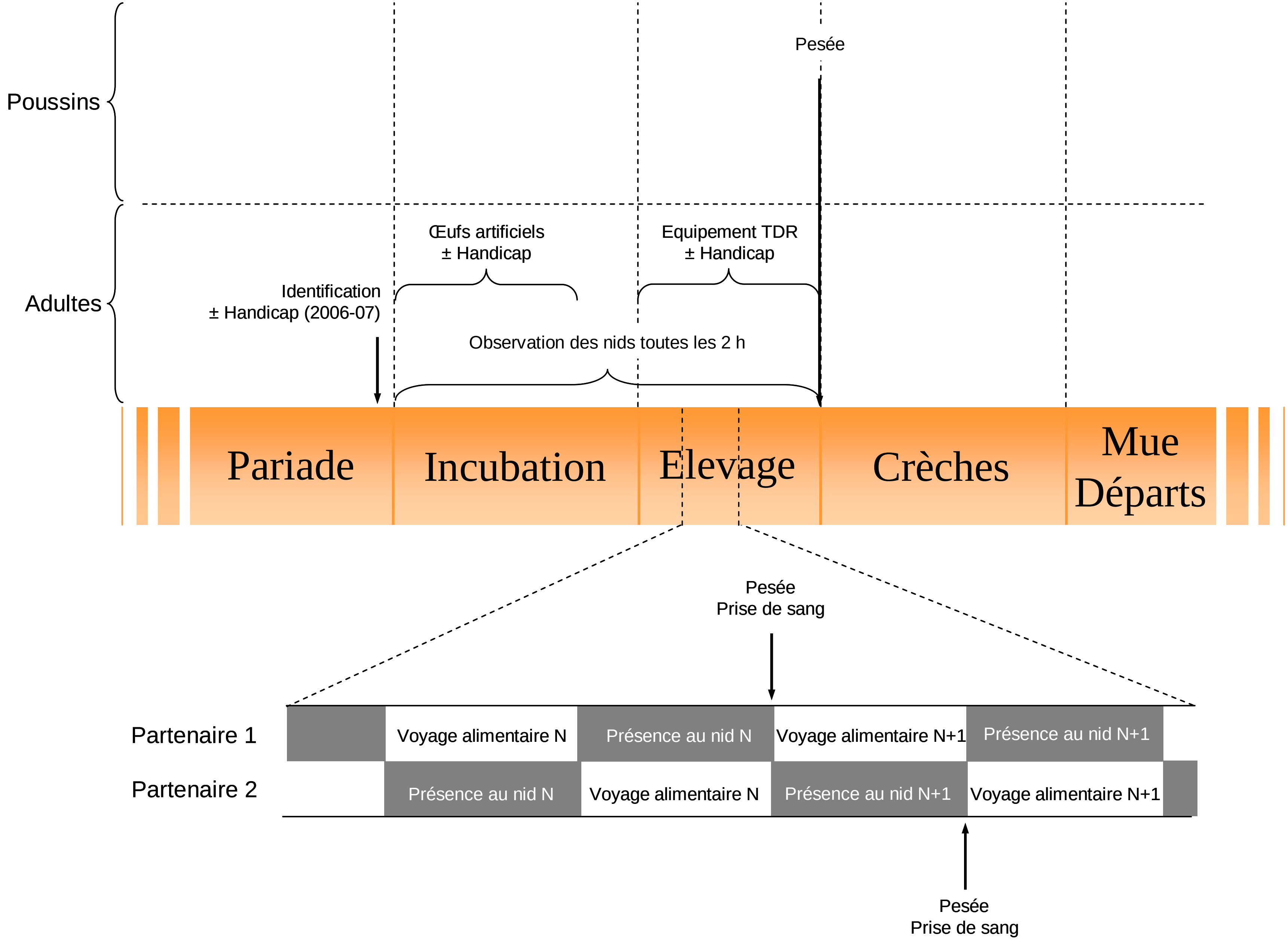


Fig. 12 : Cycle de reproduction du manchot Adélie et procédure générale lors des deux saisons de reproduction 2006-07 et 2007-08 (TDR= enregistreurs de plongée).

3

PUBLICATIONS

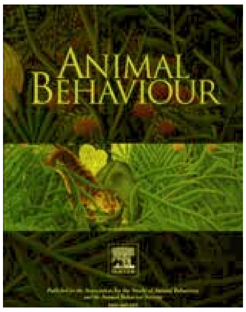
Publications

Rappels des objectifs :

- **Article 1** (contrainte expérimentale) : Evaluation de la réponse comportementale des individus handicapés et de leurs partenaires et effets à long terme sur leur survie et leur fécondité. Etude des conséquences sur les poussins en termes de succès reproducteur, de masse corporelle et de comportement envers les parents.
- **Article 2** (contrainte expérimentale) : Identification des phases critiques du cycle reproducteur susceptibles de modifier le succès reproducteur des couples handicapés.
- **Article 3** (contrainte environnementale) : Evaluation de la réponse comportementale et physiologique d'individus reproducteurs et étude des conséquences sur les poussins en termes de succès reproducteur et de masse corporelle.
- **Article 4** (contrainte expérimentale et environnementale) : Etude de la capacité de recherche alimentaire *via* le comportement de plongée.
- **Article 5** (contrainte expérimentale) : Etudes de paramètres physiologiques et alimentaires chez les individus handicapés et leurs partenaires.
- **Article 6** (contraintes expérimentale et environnementale) : Mesure des concentrations de corticostérone et de prolactine.
- **Article 7** (contrainte expérimentale) : Mesure du stress oxydant et de la dynamique des télomères chez des manchots handicapés et contrôles
- **Article 8** (contrainte environnementale) : Mise en relation du statut oxydant et des stratégies de recherche alimentaire.

CAN A HANDICAPPED PARENT RELY ON ITS PARTNER? AN EXPERIMENTAL STUDY WITHIN ADÉLIE PENGUIN PAIRS

Michaël BEAULIEU, Thierry RACLOT, Antoine DERVAUX, Yvon Le MAHO,
Yan ROPERT-COUDERT, André ANCEL



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Can a handicapped parent rely on its partner? An experimental study within Adélie penguin pairs

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In biparental species, the response of parents when their mates are disadvantaged is highly variable. Moreover, experimental studies on parental effort have mainly focused on short-lived birds whose breeding constraints largely differ from those of long-lived species such as seabirds. We investigated the short- and long-term consequences of handicapping one parent within Adélie penguin, *Pygoscelis adeliae*, pairs. We also examined whether handicapped mates and offspring could convey cues informing the other parent of the need to increase breeding effort and whether this parent adjusted its behaviour accordingly. While handicapped penguins foraged for longer and lost more mass than controls, partners, fasting for longer at the nest, did not change their behaviour or lose more mass suggesting that they compensated at least for themselves. Information exchange was increased between mates after the return of handicapped females from foraging. However, partner males did not respond to this. Handicapped-pair chicks, which were smaller than control chicks, did not increase their solicitation rate for food. In the subsequent breeding season, compared to controls, 40% of previously handicapped females laid fewer eggs, the resight rate of previously handicapped males was lower and pair instability was higher. No additional cues seemed to be detected by Adélie penguins when their mates were handicapped and, for handicapped-pair offspring, the cost associated wih a higher solicitation rate was probably too high for these small chicks to support. Consequently, we found no compensatory behaviour from partners in this long-lived species: handicapped individuals and offspring both supported the whole additional cost in both the short term and the long term.

In species where both parents provide parental care, a conflict of interest may arise between partners which are both expected to minimize current reproductive effort but are none the less forced to cooperate to breed (Houston et al. 2005). Many experimental studies on parental effort, mainly carried out on passerines (Houston & Davies 1985), have shown that parents could respond to a reduction in care by their partners, by modifying their own effort. However, depending on the species, the partners' responses may show discrepancies and vary from a decreased effort (Sanz et al. 2000) or no response (Sanz et al. 2000; Schwagmeyer et al. 2002; Tajima & Nakamura 2003) to incomplete (Velando & Alonso-Alvarez 2003; Paredes et al. 2005; Navarro & González-Solís 2007) or complete compensatory responses (Wright & Cuthill 1990; Sanz et al. 2000) and these responses may be sex biased (Sanz et al. 2000; Tajima & Nakamura 2003; Velando & Alonso-Alvarez 2003).

These species and sex-specific differences may be determined by: (1) the availability of proximate cues that indicate the reduced effort of the mate (such as the feeding need of offspring, expressed through begging behaviour, or the mate's behaviour) and the individuals' capacity to detect them (Houston et al. 2005; Johnstone & Hinde 2006); (2) the individuals' capacity to sustain additional effort, implying that the individual had not been working at its maximum capacity before; and (3) the consequences of this additional cost for survival and future breeding attempts. Indeed, animals should balance the cost of their current reproductive investment against the potential negative effects of this current reproduction on future reproductive attempts (Williams 1966; Roff 1992; Stearns 1992). Short-lived individuals with low interannual survival are thus expected to vary the level of investment in their current reproduction, and thus to compensate for a reduction in care by their partner, at the expense of their own body condition and survival. In contrast, to maximize their lifetime reproductive success, long-lived animals with high interannual survival should minimize their current reproductive effort at a level that none the less allows them to breed. They are therefore expected to invest an optimal fixed amount in current reproduction, independent of the

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current reproductive constraints (Ricklefs 1987; Mauck & Grubb 1995). In that case, if the cost of breeding increases, offspring are expected to support the whole additional cost while parents put in a constant effort.

In the present study, we examined the consequences of an experimental increase in breeding constraints in a long-lived biparental species, the Adélie penguin, *Pygoscelis adeliae*. From the methods that have been used in the field (reviewed is Hinde 2006), we selected one that reduces the hydrodynamic properties of the animal. Externally fitted equipment affects diving behaviour if the cross-sectional area (CSA) of the equipment represents more than 1% of the animal's CSA (Culik & Wilson 1991). Among diving animals, penguins are particularly appropriate for manipulating breeding cost through an increase in their foraging cost while at sea as these birds are extremely streamlined. Their breeding behaviour has been well studied and effects of external handicaps are predictable (Ropert-Coudert et al. 2007). We investigated the responses of both the handicapped individual and its partner over short and long timescales. To explain why the partner would or would not compensate, we focused on the exchange of information between mates during nest relief and from the chicks to the adults. For this purpose, we first investigated the direct effects of a handicap on the time budget and changes in body mass in handicapped individuals and their partners. Second, we examined the indirect effects of a handicap on chicks, in terms of reproductive success, chick body mass and chick behaviour. Finally, to investigate the long-term consequences of previously increased breeding constraints, the same pairs were monitored during the subsequent breeding season.

METHODS

Study Species and Area

Adélie penguins breed during the austral summer. Females lay one or two eggs and generally leave the first incubation shift to the male while they feed at sea. About 12 days later, they take the second incubation shift for the same duration. Incubation lasts on average 34 days. After the eggs have hatched, both adults take turns to forage at sea and attend the chick at the nest. After returning from a foraging trip, during nest relief ceremonies, both birds stand and wave their necks back and forth while uttering a loud cackling call with open bill. This behaviour, called 'loud mutual display' (LMD), is related to the readiness to switch roles at the nest and the number of LMDs during the first 30 s indicates more information exchanges than during the remainder of the relief time (Müller-Schwarze & Müller-Schwarze 1980). After 3–4 weeks of the guarding stage, chicks become mobile and parents continue to feed their offspring irregularly for a few weeks until fledging (crèche stage).

In this study, we focused on the incubation and the guarding stages since it was impossible to monitor the birds regularly during the crèche stage. The study was conducted in Dumont d'Urville (66°40′S, 140°01′E), Adélie Land, Antarctica during the austral summers 2006–2007 and 2007–2008 and was approved by the ethic committee of the French Polar Institute (IPEV) and the Terres Australes et Antarctiques Françaises (TAAF).

Summer 2006–2007

We followed 46 pairs: 16 pairs were assigned to the control group and 30 to the treated group in which one member of the pair was handicapped (further referred to as handicapped bird) while the other remained untreated (further referred to as partner bird). Such a design meant that three pair groups were used (control pairs, handicapped-female pairs and handicapped-male pairs); each pair group comprised males and females, resulting in six bird groups (Table 1).

At the end of the courtship period, birds were captured on their nest and weighed with an electronic balance (Ohaus, ±2 g). Body mass changes thereafter were calculated considering this first weighing as the reference (100%). The left flipper (from the humeral head to the tip of the outstretched flipper) was measured with a ruler (±1 mm). Birds were identified with a Nyanzol-D mark painted on the breast feathers and with a subcutaneous passive transponder (31.2 × 3.8 mm, 0.8 g, Texas Instruments TIRIS, Dallas, TX, U.S.A.). To insert the transponders, we followed the procedure described by Renner & Davis (2000): the sterile transponder was injected with a needle cleaned with iodine solution before each injection. In addition, to avoid the transponder migrating into the penguin's body, it was injected in the lower part of the bird (i.e. in the loose skin between the tail and the left thigh). The procedure took only a few minutes and did not require sedating the birds. No complications have been related to the insertion of the transponder. This procedure is known to be safe and reliable (Renner & Davis 2000); it can be used for the lifetime of the bird and therefore in long-term studies (Dugger et al. 2006). For these reasons, the transponders were not removed at the end of the experiment, so we could monitor identified birds year after year.

To handicap penguins, we used dummy Plexiglas devices. They were attached with mastic, cyanoacrylate glue, Tesa tape and cable ties to the middle-back feathers. Our devices were parallelepipeds (2.5 × 3.5 × 6.0 cm) and weighed 60 g; this size was chosen not to be too deleterious for birds and was comparable to the size of devices known to have negative effects on Adélie penguins (e.g. longer foraging trips, increased mass loss, decreased provisioning rate and lower breeding success; Wilson et al. 1989; Culik & Wilson 1991, 1992; Watanuki et al. 1992; Miller & Davis 1993). Handicapped birds were then released close to their nest. Two days later (to minimize disturbance from consecutive captures on the same nest), the partner underwent a similar treatment except for the attachment of the device. Penguins were captured and weighed only once more during the guarding stage, 40–45 days after laying.

The 46 nests were observed from a distance for periods ranging from 10 min to 2 h to monitor copulation behaviours, laying, foraging trip duration and reproductive success. Laying date was considered as the laying date of the first egg. Provisioning rate was defined from the chick's perspective and was calculated as the number of parental returns (male + female) from the sea. The final reproductive success was approximated by the number of chicks surviving until the crèche stage since, at this stage, chick mortality is very rare (Davis & McCaffrey 1986; Clarke et al. 2002). Penguins were sexed by a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962; Kerry et al. 1993).

During the guarding stage, we filmed 39 returns from a foraging trip from a distance to examine LMD, solicitations and chick feeding in each group. Observations were limited to the first 1.5 h since, in penguins, most chick feeding occurs soon after the return of a parent from the sea, over a relatively short period, usually of less than 1 h (Taylor 1962; Williams 1982). Over the duration of the video record, we counted both chick solicitations and feeding events. Solicitations were considered successful if they resulted in a feeding bout and unsuccessful if not. In the case of successful solicitations, we checked that parents regurgitated with characteristic heaves of their body. Feeding was analysed by the number of feeding events and the total time that adults spent feeding (Van Heezik & Seddon 1996) since this duration includes both the number and the duration of feeding events and should approximate the amount of food given better than the two parameters

Table 1
Breeding parameters in the season when the handicap was used (Year *N*)

	Control males (*N*=16)	Control females (*N*=16)	Partner males (*N*=13)	Handicapped females (*N*=13)	Handicapped males (*N*=17)	Partner females (*N*=17)
Wing length (mm)	198±2	191±2	197±2	189.15±1.78	193.06±1.56	191.18±1.56
Courtship body mass (kg)	5.33±0.10	4.58±0.10	5.16±0.10	4.69±0.10	5.06±0.12	4.55±0.12
% CSA	—	—	—	4.22±0.06	3.88±0.05	—
Laying date	—	17 Nov±0.58 days	—	18 Nov±0.88 days	—	18 Nov±0.66 days
First foraging trip duration (days)	11.90±0.46	11.52±0.46	10.09±0.51	**13.63±0.51**	**14.82±0.47**	10.91±0.44
Foraging trip duration (guarding, days)	0.97±0.03	1.02±0.03	1.02±0.05	**1.83±0.05**	**1.62±0.16**	1.05±0.04
Time together on the nest (days)	5.67±0.36		**2.71±0.39**		**4.06±0.49**	
No. of eggs per pair	1.87±0.08		1.85±0.10		1.75±0.11	
No. of chicks per pair*	1.19±0.13		1.08±0.13		**0.59±0.12**	
Chick age (days)*	25.87±0.87		23.92±0.93		22.50±1.07	
Brood mass (kg)*	3.09±0.15		**1.93±0.16**		**1.38±0.18**	
No. of provisionings*	22.27±1.22		**15.25±1.13**		**15.75±1.40**	
Total no. of solicitations†	72.37±18.89		76.92±12.50		30.81±9.76	
Duration of solicitations (s)†, ‡	7.23±0.48		6.46±0.40		9.61±1.44	
Duration of feeding events (s)†	3.42±0.22	4.41±0.35	3.49±0.24	3.79±0.28	**4.37±0.16**	4.92±0.22
No. of feeding events†	21.53±6.28	12.96±4.79	21.26±10.36	23.86±4.19	16.57±6.60	8.14±0.74
No. of feeding events†, §	19.04±2.24	16.36±6.00	16.74±3.70	19.85±2.69	20.43±4.66	17.89±2.93
No. of feeding events†	19.06±4.61		22.51±4.65		12.26±3.85	
No. of feeding events†, §	18.37±2.88		18.34±2.36		19.49±3.16	
Total feeding duration (s)†	68.18±28.93	53.69±30.12	91.06±31.07	98.98±26.93	70.13±39.45	35.42±39.36
Total feeding duration (s)†, §	64.54±20.77	49.40±21.84	86.84±21.80	82.81±18.74	87.89±21.80	67.64±29.39
Total feeding duration (s)†	61.79±19.71		95.37±19.76		52.77±25.67	
Total feeding duration (s)†, §	57.77±14.72		83.69±18.67		78.43±19.83	

Results are expressed as means ± SE. % CSA = cross-sectional area of the handicap/cross-sectional area of the bird. Numbers in bold indicate a significantly different result ($P < 0.05$) between the group considered and its respective control.

* Data obtained at end of the guarding stage.

† Data obtained in first 1.5 h after return of parent.

‡ Only successful solicitations were taken into account.

§ Data calculated with total number of solicitations as a covariate.

separately. The duration of each feeding bout was defined as the time elapsed between the chick's bill insertion into the parent's mouth until withdrawal.

At the end of the guarding stage, the chicks were quickly and lightly sprinkled with paint (Raidex, Raidex GmbH, Dettingen/Erms, Germany) for individual recognition when left unguarded for the first time. This nontoxic paint remained only a few days on the down of chicks and had no obvious effect on the chicks' or the adults' behaviour. At the same time they were weighed with a spring balance (Salter, ±20 g).

To avoid the stress of additional capture of adult penguins, dummy devices were left on the birds until the moult, at the end of the austral summer, when the device fell off with the feathers to which it was attached.

Summer 2007–2008

At the end of the courtship period the following summer, we checked with a manual antenna all the nests that had been occupied by experimental pairs in 2006–2007 to search for penguins identified with a transponder. In addition, all the nests in the subcolony and in adjacent subcolonies ($N \approx 330$ nests) were checked twice more during the male and female incubation shifts. Previously manipulated birds as well as their new partner (if they formed a new pair) were identified and weighed with the same procedure as that in 2006–2007. For the rest of the breeding cycle, the procedure was the same as described in 2006–2007 with the difference that no bird was handicapped.

Data Analysis

Direct and indirect effects of the handicap were analysed in 2006–2007 and in 2007–2008. As foraging trip durations during incubation and the guarding stage are not comparable in Adélie penguins, comparisons between groups were carried out independently for the first foraging trip during incubation and for all foraging trips during the guarding stage. For video analyses we used The Observer Video Pro (Noldus Information Technology, Wageningen, The Netherlands). Solicitations were compared between the three pair groups to examine the overall chick need. In contrast, feeding parameters were compared both between the three pair groups and between the six bird groups (sex*status interaction). In 2007–2008, only stable pairs that had raised at least one chick successfully in 2006–2007 were included in the comparisons. Resight and divorce rates (and, thus, pair stability) were calculated. A divorce occurred when both members of a pair were resighted but were not breeding together. A pair was considered as not stable if one member did not return to the colony or divorced.

To compare groups (first foraging trip duration, body mass, body mass changes, wing length, laying date, time spent together by partners at the nest, age and masses of chicks and feeding duration), we used general linear models (GLM) and general linear mixed models (GLMM, in the case of repeated measures) which allow pseudoreplication to be taken into account by including a random and a repeated factor. Normality of residuals was assessed using a Shapiro–Wilk test. If this latter condition was not fulfilled, generalized estimating equations (GEE) were used, with a gamma distribution (foraging trip duration during the guarding stage, duration of solicitations). Generalized linear models (GzLM) or GEE (in the case of repeated measures) with a Poisson distribution were also used for count data (provisioning rate, number of LMDs, solicitations, feeding events and reproductive success). Multiple comparisons were undertaken using the post hoc Bonferroni test. Chi-square and Fisher's exact tests were used to compare return and divorce rates and pair stability. The same tests were used to compare the proportion of females that reduced their clutch size between the two breeding seasons. Spearman correlations were used to test the relationship between the number of LMDs and the time elapsed between the arrival of one parent and the departure of the other parent, and between the number of chick solicitations and feeding (number of feeding events and total duration of feeding).

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL, U.S.A.). Results are expressed as means ± SE and the significance level was set at $\alpha = 0.05$.

RESULTS

Sex of Experimental Birds

In 2006–2007, the sex of the 92 individuals initially determined by cloacal inspection and copulation behaviour was first confirmed by examination of the incubation routine and afterwards in the subsequent season (2007–2008) even when identified individuals changed mate. In 2006–2007, 13 females and 17 males were handicapped in the treatment group (Table 1).

Effects of Handicap During Breeding Season

Intergroup differences

Male and female wing length and body mass were significantly different (GLM: $F_{1,86} = 18.40$, $P < 0.001$; $F_{1,83} = 52.65$, $P < 0.001$, respectively). The device's CSA as a proportion of the handicapped birds' CSA was significantly less important in males than in females (GLM: $F_{1,28} = 20.20$, $P < 0.001$). Importantly, within male and female groups, wing length (GLM: $F_{2,86} = 0.80$, $P = 0.45$), body mass (GLM: $F_{2,83} = 0.55$, $P = 0.58$) and laying date (GLM: $F_{2,40} = 0.392$, $P = 0.39$) did not differ between control, handicapped and partner birds (Table 1), so these groups were considered to be comparable for the following analyses.

Time budget

The experiment affected the time budget of the handicapped birds: the duration of the first foraging trip during incubation was affected by the status (GLM: $F_{1,84} = 33.51$, $P < 0.001$), with handicapped penguins performing longer foraging trips (14.22 ± 0.35 days) than controls (11.21 ± 0.32 days; $P < 0.001$) and partners (10.50 ± 0.34 days; $P < 0.001$). The same trend was observed during the guarding stage (GEE: Wald $\chi^2_2 = 70.13$, $N = 733$, $P < 0.001$), with handicapped penguins performing longer foraging trips (1.73 ± 0.08 days) than controls (1.00 ± 0.02 days; $P < 0.001$) and partners (1.03 ± 0.03 days; $P < 0.001$; Table 1).

Over the study period, control mates remained together for longer on the nest (GLM: $F_{2,33} = 15.77$, $P < 0.001$) than mates in handicapped-female pairs ($P < 0.001$) and mates in handicapped-male pairs ($P = 0.04$; Table 1). During nest reliefs, the information exchange was also affected by the experimental procedure: the number of LMDs during the first 30 s was negatively correlated with the time elapsed between the return to the nest of males and the departure of females (Spearman correlation: $r_S = -0.50$, $N = 19$, $P = 0.03$) but this was not observed after female returns ($r_S = -0.09$, $N = 20$, $P = 0.71$; Fig. 1a). The interaction between sex and status had an influence on the occurrence of LMDs during the first 30 s after returning (GzLM: Wald $\chi^2_2 = 17.80$, $N = 39$, $P < 0.001$) with more LMDs observed after the return of handicapped females than after the return of control ($P = 0.02$) and partner females ($P < 0.001$). In contrast, the return of any male (control, partner or handicapped) was followed by the same number of LMDs (all $P = 1.00$; Fig. 1b).

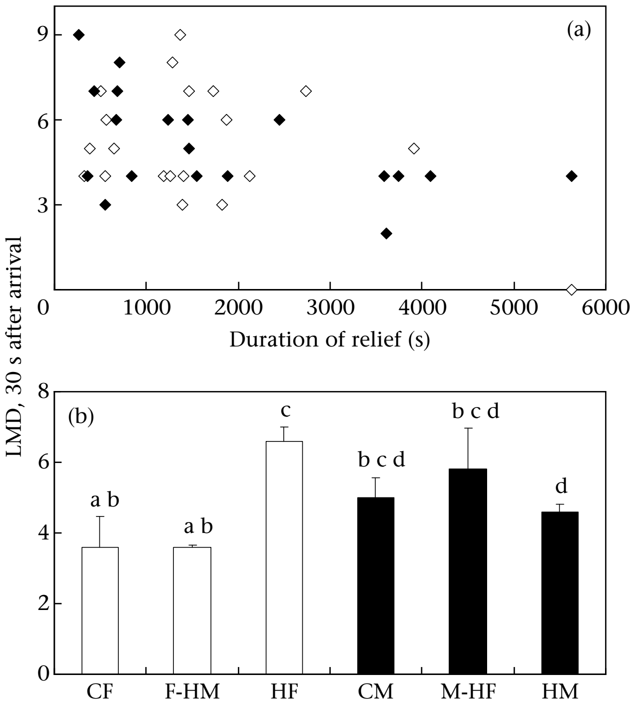

Figure 1. (a) Relationship between the number of loud mutual displays (LMDs) during the first 30 s of a nest relief and the duration of nest relief after a male returned (black diamonds) and after a female returned (white diamonds). (b) Number of LMDs after the return of control females (CF), handicapped-male females (F-HM = partner females), handicapped females (HF), control males (CM), handicapped-female males (M-HF = partner males) and handicapped males (HM). Different letters indicate significant differences between groups ($P < 0.05$).

Body mass changes

Body mass changes between the courtship and the guarding stage did not differ between sexes (GLM: $F_{1,64} = 0.45$, $P = 0.50$) but were significantly different between the three statuses (GLM: $F_{1,64} = 10.06$, $P < 0.001$) with control and partner penguins weighing 91.3 ± 1.0% and 91.2 ± 1.1% of their initial body mass, respectively, while handicapped birds weighed 85.3 ± 1.1% of their initial body mass ($P < 0.001$ and $P = 0.001$, respectively; Fig. 2). The sex*status interaction was not significant (GLM: $F_{1,64} = 0.10$, $P = 0.91$).

Reproductive success and chick body mass

Reproductive success was significantly different between groups (GzLM: Wald $\chi^2_2 = 7.56$, $N = 46$, $P = 0.02$) and was highly affected by the handicap: while the number of eggs laid was the same in each group (all $P > 1.00$), the number of chicks differed at the end of the guarding stage with fewer chicks produced in handicapped-male pairs ($P = 0.01$; Table 1).

At the end of the guarding stage, even though handicapped-pair chicks were left alone for the first time by their parents earlier than control chicks, this difference was not significant (GLM: $F_{2,35} = 3.08$, $P = 0.06$). Brood mass differed between groups (GLM: $F_{2,35} = 29.86$, $P < 0.001$): control broods weighed significantly more than handicapped-male broods ($P < 0.001$) and handicapped-female broods ($P < 0.001$; Table 1). The lower body mass of handicapped chicks was associated with a lower provisioning rate during the guarding stage. Total provisioning differed between pair groups (GzLM: Wald $\chi^2_2 = 20.69$, $N = 35$, $P < 0.001$) with handicapped-male and handicapped-female pairs provisioning at lower rates than control pairs ($P < 0.001$ and $P = 0.001$, respectively; Table 1).

Since one chick may die during the guarding stage, the same comparisons were performed for pairs that had only one chick during the entire guarding stage. Chicks from handicapped-male pairs were left by parents at a younger age at the end of the guarding stage (GLM: $F_{2,17} = 6.45$, $P = 0.008$): they were 22.4 ± 0.9

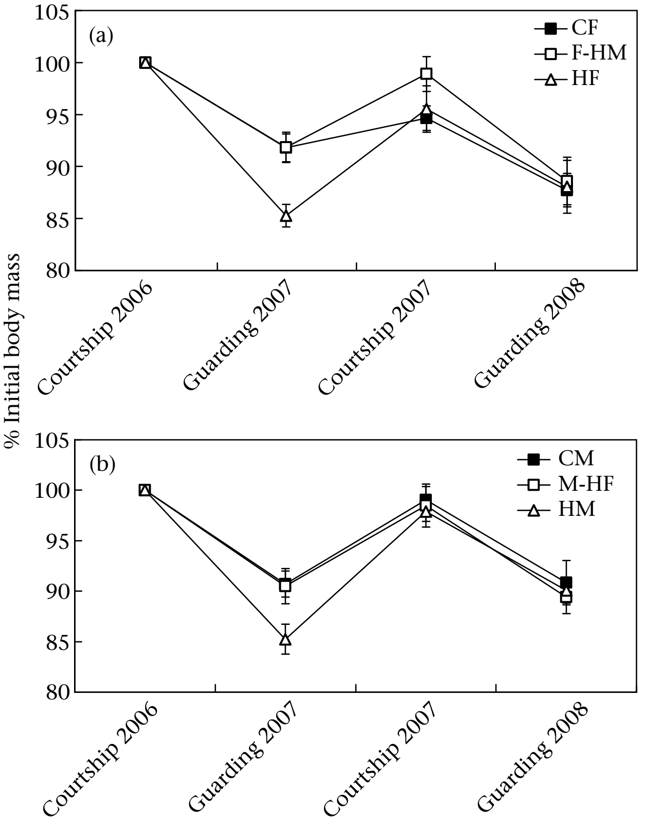

Figure 2. Body mass changes (%) along the study period in (a) females and (b) males. CF: control females; F-HM: handicapped-male females (=partner females); HF: handicapped females; CM: control males; M-HF: handicapped-female males (=partner males); HM: handicapped males.

days old while control chicks were 27.3 ± 1.1 days old ($P = 0.008$) and handicapped-female chicks were 25.5 ± 1.1 days old ($P = 0.12$). Control chicks were significantly heavier (GLM: $F_{2,17} = 25.14$, $P < 0.001$) than handicapped-male chicks ($P < 0.001$) and handicapped-female chicks ($P = 0.007$; Fig. 3a). Moreover, handicapped-male chicks were significantly lighter than handicapped-female chicks ($P = 0.01$). When we controlled for provisioning rate and chick age, the status still had an influence on chick body mass (GLM: $F_{2,13} = 8.46$, $P = 0.004$) but the difference was only found between handicapped-male chicks and control chicks ($P = 0.008$) and between handicapped-male chicks and handicapped-female chicks ($P = 0.02$; Fig. 3b).

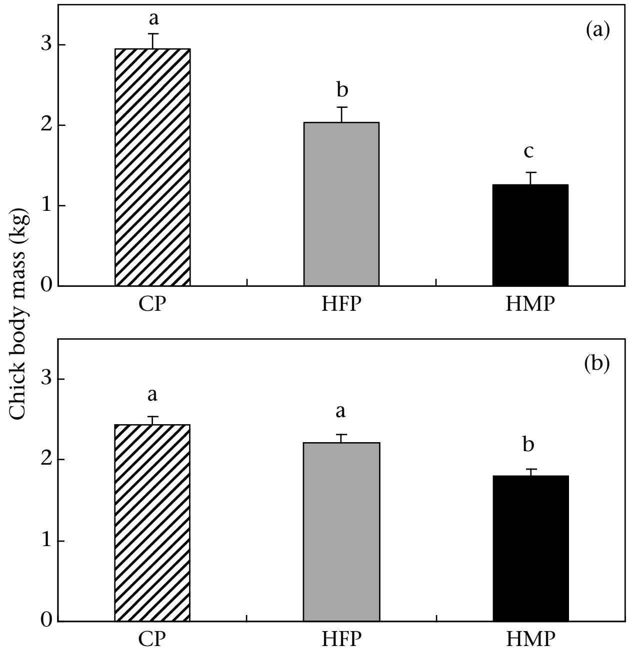

Figure 3. (a) Chick body mass and (b) chick body mass with provisioning rate and chick age as covariates in control pairs (CP), handicapped-female pairs (HFP) and handicapped-male pairs (HMP). Different letters indicate significant differences between groups ($P < 0.05$).

Chick solicitations and parental feeding

During the 39 video recordings of the first 90 min of visits, 2454 solicitations and 726 feeding events were observed. When we controlled for the number of chicks, handicapping a parent affected the number of chick solicitations (GzLM: Wald $\chi^2_2 = 10.58$, $P = 0.005$): handicapped-male chicks solicited half as many times as handicapped-female chicks ($P = 0.005$) and control chicks although this difference was not significant ($P = 0.11$; Table 1). Successful solicitations were on average 3 s (40%) longer than unsuccessful solicitations (GEE: Wald $\chi^2_2 = 49.87$, $P < 0.001$; Fig. 4a) but were not different between groups (GEE: Wald $\chi^2_2 = 5.22$, $P = 0.07$; Table 1). In contrast, the mean duration of feeding events differed between groups (GEE: Wald $\chi^2_2 = 14.43$, $P < 0.001$): feeding events from handicapped males were longer than those from control and partner males ($P = 0.001$ and $P = 0.05$, respectively; Table 1). Chick solicitations can be considered as the main initiator of parent feeding since the number of solicitations was positively correlated with the number of feeding events (Spearman correlation: $r_S = 0.83$, $N = 39$, $P < 0.001$) and the total time spent feeding by adults ($r_S = 0.77$, $N = 39$, $P < 0.001$; Fig. 4b). However, the total number of feeding events and total feeding time were not significantly different between groups (GEE: Wald $\chi^2_2 = 2.83$, $P = 0.24$; GLMM: $F_{2,14} = 0.67$, $P = 0.53$, respectively; Table 1) even though handicapped males and partner females were feeding their offspring less. When we controlled for solicitation rate, this trend

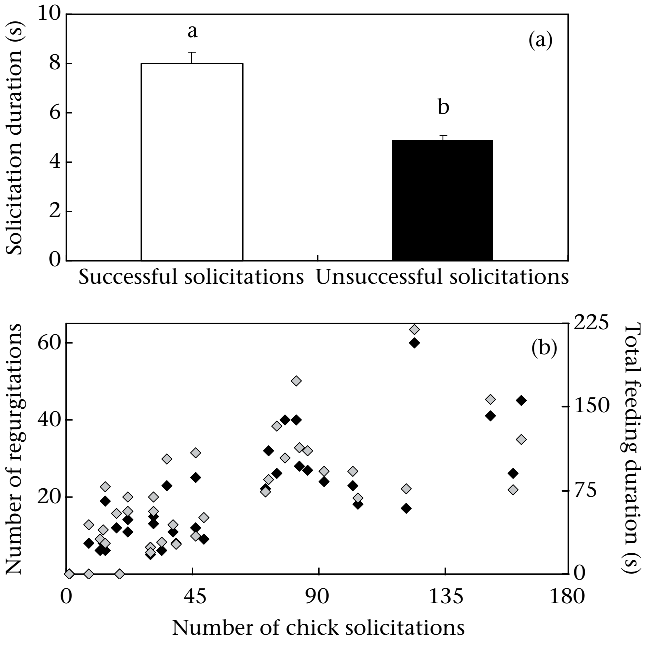

Figure 4. (a) Duration of successful and unsuccessful chick solicitations and (b) relationship between the number of solicitations and the number of feeding events (black diamonds) from parents and total duration of feeding (grey diamonds). Different letters indicate significant differences between groups ($P < 0.05$).

Table 2
Breeding parameters 1 year after the handicap was used (Year $N + 1$)

	Control males (N=16)	Control females (N=14)	Partner males (N=12)	Handicapped females (N=12)	Handicapped males (N=12)	Partner females (N=12)
Resighted individuals (%)	100.00	87.50	92.31	92.31	**70.59**	70.59
Divorce (%)	14.29		18.18		37.50	
Pair stability (%)	75.00		69.23		**29.41**	
Laying date	—	19 Nov±1.05 days	—	19 Nov±1.07 days	—	19 Nov±0.04 days
No. of eggs per pair	2.00±0.40		1.58±0.36		1.87±0.48	
No. of chicks per pair*	1.20±0.34		1.11±0.35		1.25±0.56	
Chick age (days)*	28.78±2.07		28.37±2.20		29.00±2.78	
Brood mass (kg)*	3.02±0.34		2.69±0.36		2.76±0.46	
No. of provisionings*	20.78±1.52		20.88±1.62		20.20±2.01	

Results are expressed as means ± SE. Numbers in bold indicate a significantly different result ($P < 0.05$) between the group considered and its respective control.
* Data obtained at end of guarding stage.

disappeared (number of feeding events: GEE: Wald $\chi^2_2 = 0.41$, $P = 0.81$; time spent feeding; GLMM: $F_{2,14} = 0.04$, $P = 0.96$; Table 1). We can thus conclude that after a parent returns, partners did not show compensatory feeding behaviour in response to the lower provisioning rate of their handicapped partner.

From the offspring's perspective, handicapped and control chicks were fed similarly after a parent returned (number of feeding events: GEE: Wald $\chi^2_2 = 2.83$, $P = 0.24$; total time spent being fed: GLMM: $F_{2,16} = 0.96$, $P = 0.40$) even though the feeding rate and feeding duration of handicapped-male chicks were the lowest of all groups. That trend was none the less suppressed after we controlled for the number of chick solicitations (number of feeding events: GEE: Wald $\chi^2_2 = 0.13$, $P = 0.94$; time spent being fed: GLMM: $F_{2,17} = 0.78$, $P = 0.47$; Table 1).

Effects of Handicap in Subsequent Breeding Season

Return rate and pair stability

Handicapped-male pairs were significantly less stable than control pairs (Fisher's exact test: $P = 0.02$) but not handicapped-female pairs (Fisher's exact test: $P = 0.06$; Table 2). Resight rates for males and females did not differ (89.1% and 82.6%, respectively; chi-square test: $\chi^2_1 = 0.36$, $P = 0.77$) and resight rates between control, partner and handicapped birds in males and females were equivalent (Fisher's exact tests: $P > 0.05$) with the exception that handicapped males returned to the colony less than control males (Fisher's exact test: $P = 0.04$; Table 2). Although divorces occurred twice as often in handicapped-male pairs as in control pairs, divorce proportions were not significantly different between groups (Fisher's exact tests: all $P > 0.05$; Table 2).

Body mass changes

The handicap procedure had no long-term effects on body mass: relative to initial body mass measured during courtship in 2006–2007, penguin body mass during the courtship and the guarding stage in 2007–2008 did not differ between the sexes (GLMM: $F_{1,110} = 2.35$, $P = 0.13$) and the statuses (GLMM: $F_{1,110} = 0.17$, $P = 0.85$) and the sex*status interaction was not significant (GLMM: $F_{2,110} = 0.68$, $P = 0.51$; Fig. 2).

Reproductive success and chick body mass

All the female groups laid a similar number of eggs (GzLM: Wald $\chi^2_2 = 0.61$, $N = 32$, $P = 0.74$) on about the same date (GzLM: $F_{2,16} = 0.11$, $N = 32$, $P = 0.89$; Table 2). Nevertheless, compared to the laying in 2006, 41.7% of handicapped females laid fewer eggs while no control or partner females decreased their clutch size (Fisher's exact tests: $P = 0.04$ and $P = 0.11$, respectively). In contrast, 8.3% of handicapped females increased their clutch size while 16.7% of control females and 14.3% of partner females laid more eggs (Fisher's exact tests: all $P < 0.001$; Fig. 5). Reproductive success was the same in each group (GzLM: Wald $\chi^2_2 = 0.06$, $N = 23$, $P = 0.97$), brood mass (GLM: $F_{2,19} = 0.25$, $P = 0.78$) and age at the end of the guarding stage (GLM: $F_{2,19} = 0.02$, $P = 0.98$) did not differ between groups and chicks were provisioned at similar rates (GzLM: Wald $\chi^2_2 = 0.08$, $N = 22$, $P = 0.96$; Table 2).

Effects of pair instability

From 2006 to 2007, 25 pairs were stable while 22 were newly established. No differences between the two groups were found. Their body masses were similar during courtship in 2007 in males and females (sex*stability interaction: GLM: $F_{1,82} = 0.001$, $P = 0.98$) and they lost mass at the same rate (sex*stability interaction: GLM: $F_{1,71} = 0.006$, $P = 0.94$). The number of chicks at the end of the guarding stage was lower than the number of eggs in both groups (GzLM: Wald $\chi^2_2 = 56.67$, $P < 0.001$) but the numbers of eggs (1.88 ± 0.90 and 1.82 ± 0.10, respectively) and chicks (1.12 ± 0.12 and 0.96 ± 0.13, respectively) were equivalent between the two groups (all $P > 0.05$). The brood mass was similar in stable and newly established pairs (2.84 ± 0.20 kg and 2.68 ± 0.22 kg, respectively; GLM: $F_{1,38} = 0.27$, $P = 0.61$). Chicks were provisioned at similar rates over the guarding stage (20.7 ± 1.0 and 19.8 ± 1.1 visits, respectively; GzLM: Wald $\chi^2_1 = 0.40$, $N = 40$, $P = 0.53$) and had similar ages at the end of this period (28.68 ± 1.26 and 27.44 ± 1.39 days, respectively, GLM: $F_{1,38} = 0.44$, $P = 0.51$).

DISCUSSION

Effects of Handicap During Breeding Season

Overall, the results of our study indicate that male and female Adélie penguins were affected by the handicap, and their chicks were smaller than control chicks especially in handicapped-male

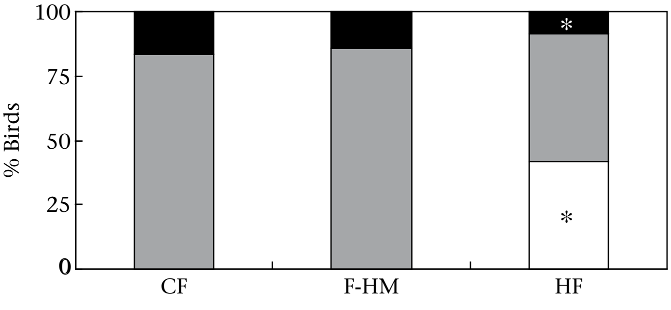

Figure 5. Percentage of birds for which clutch size increased (black), remained stable (grey) or decreased (white) between 2006 and 2007, in control females (CF), handicapped-male (=partner) females (F-HM) and handicapped females (HF). $^*P < 0.05$.

pairs. In addition, no compensatory behaviour from the partners towards their offspring was seen.

Handicapped birds did not feed their offspring less than the controls after returning from a foraging trip. This suggests that handicapped parents returned to their breeding site when their stomach was full. However, because of a lower provisioning rate (at least), handicapped chicks, and especially handicapped-male chicks, were smaller than controls. When we controlled for provisioning rate, only handicapped-male chicks remained smaller than control chicks suggesting that the lower body mass of handicapped-female chicks was caused only by the lower provisioning rate. Handicapped-male chicks were the smallest, presumably because they were fed less after a parent returned (although not significantly). It is also likely that the quality of their food had changed and handicapped males may have been forced to select lower quality prey. Since males feed more extensively upon fish than females (Clarke et al. 1998), handicapped males may have been limited to prey upon krill which is less energetically valuable than fatty fish (Watanuki et al. 2002; Ainley et al. 2003) which promote growth in penguin chicks (Heath & Randall 1985). For this purpose, further qualitative analyses on the birds' diet would be worthwhile.

The increased foraging trip duration of handicapped birds obliged their partners to fast for longer than the controls. As a consequence, the partners had an additional energetic debt when returning to the sea to feed. Assuming that the rate of prey capture was similar in partners and controls, there are several possibilities for the partners to adapt to this additional cost: they could (1) stay longer at sea to increase the net energy gain, (2) return with a lower body mass or (3) feed their chicks less. In our study, partners did not modify their foraging trip duration, their body mass loss was equivalent to that of controls and their feeding behaviour towards chicks was not modified. In Adélie penguins, the time spent fasting before foraging does not affect foraging trip duration (Davis 1988; Miller & Davis 1993). In a previous study conducted on Adélie penguins, Watanuki et al. (1992) concluded that partners did not increase foraging effort in response to a decreased parental investment by their mates. Our conclusion is different: to keep body mass and feeding rate equivalent to controls without increasing foraging trip duration, partners had to increase the rate of prey capture and consequently their foraging effort. In other words, our results suggest that partners compensated for their mate's deficiency, at least for themselves. To support this hypothesis, it would be worth conducting studies examining their at-sea behaviour with the use of miniaturized data loggers such as time–depth recorders and GPS.

However, partners did not compensate by provisioning more frequently or by feeding their offspring more than control birds. This suggests that the cost imposed by potential compensatory behaviour would be too high for subsequent breeding attempts in this long-lived species. Another reason may be that partners lacked information from their mate and their offspring (Johnstone & Hinde 2006). The return of handicapped females produced more LMDs than that of control females, as if the exchange of information was increased between mates when females were handicapped. However, males were not responsive to the number of LMDs after the return of females. In contrast, females were responsive to the number of LMDs after the return of males, but the exchange of information was not increased between mates when males were handicapped. These discrepancies between the information transmitter and the information receiver did not seem to lead the partners to consider the disadvantage of handicapped birds. In addition, handicapped-pair chicks were expected to solicit their parents more as they had a lower body mass (Iacovides & Evans 1998; Kitaysky et al. 2000). As in other bird species (Kilner 1995; Roulin et al. 2000), Adélie penguins respond positively to an increase in solicitations from their chicks and because of the strong correlations between the number of chick solicitations and adult feeding, chicks can be regarded as the main initiators of feeding. However, chicks from handicapped pairs did not solicit for food more often than control chicks and handicapped-male chicks solicited even less. Consequently handicapped-male chicks were fed less than other chicks (although not significantly). However, when we controlled for the number of chick solicitations, this trend disappeared. This suggests that if handicapped-male chicks were the smallest, it is also because they did not succeed in soliciting enough to obtain the necessary amount of food to grow normally. Handicapped chicks may not have been strong enough to sustain the cost of additional and/or longer solicitations for food. Indeed, begging is a costly activity for chicks (Verhulst & Wiersma 1997; Kilner 2001). In our study, the duration of chick solicitations importantly influenced the occurrence of consecutive feeding bouts, suggesting that successful solicitations are more costly to sustain than unsuccessful ones. To obtain food, chicks therefore have to be vigorous enough to 'persuade' their parents to give them food. In addition, handicapped-male chicks solicited less than handicapped-female chicks, suggesting that even though both groups had an increased need, handicapped-female chicks were still more vigorous than handicapped-male chicks.

Effects of Handicap in Subsequent Breeding Season

At the individual level, the handicap had deleterious consequences for females, with more than 40% of previously handicapped females decreasing their clutch size. This suggests that handicapped females put in more effort during the previous breeding season and almost half of them were not able to replenish their reserves fully during the winter. This may also be true for handicapped males whose resight rate on the colony was lower than that of control males because of an increase in mortality rate in winter, dispersion to other colonies or skipping of the breeding season. At the pair level, the main consequence was pair instability in previously handicapped-male pairs (Table 2). This pair instability was the result of both nonreturns and divorces. Divorces may also have affected pair stability since breeding failure was much higher in handicapped-male pairs than in other groups. Indeed, unsuccessful breeders often divorce their mates (Ens et al. 1996; Dubois & Cézilly 2002; Moody et al. 2005) and information on breeding performance can influence decisions for more than a year (Naves et al. 2006). Moreover, Lewis et al. (2006) demonstrated that, in species with biparental care, behavioural determinants of quality operated essentially on the time mates spent together at the nest site. In our study, pair bonds may have been weakened in handicapped pairs for which mates spent less time together and especially in handicapped-male pairs whose breeding success was strongly diminished during the year of the handicap experiment.

Finally, previously handicapped pairs behaved similarly to control pairs and had the same reproductive success as controls. Reproductive success was also equivalent between stable and newly established pairs so that the handicap experience in year N had no direct or indirect effects on the reproductive success in year $N+1$ and the long-term cost may have been mainly transferred to chicks in year N.

CONCLUSION

In Adélie penguins, when one mate was handicapped, no compensatory care was observed from the partner. This was probably because (1) the cost of such a behaviour would have been too high for subsequent breeding attempts in this long-lived species and (2) partners could not detect cues from their mate or their offspring, informing them of the need to put in more breeding effort. As a consequence, handicapped individuals and offspring both supported the whole additional breeding cost of the handicap. In this study, we investigated long-term consequences for adults and we showed that the handicap may affect the return rate of handicapped males, pair stability and clutch size during the subsequent season. However, the examination of long-term consequences for chicks, which also had to support the extra cost, would be of great interest; for instance, to what extent the early growth condition of the handicapped-pair chicks would affect their survival and breeding performance when adults remains to be investigated.

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Article 2 : Effets de la contrainte expérimentale sur le succès d'éclosion

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ADVERSE EFFECTS OF INSTRUMENTATION IN INCUBATING ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*)

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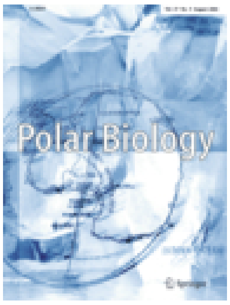

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ORIGINAL PAPER

Adverse effects of instrumentation in incubating Adélie penguins (*Pygoscelis adeliae*)

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Abstract The use of data-loggers has permitted to explore the biology of free-ranging animals. However, this method has also been reported to reduce reproductive success while the reasons of this deleterious effect remain poorly documented. In this study, we aimed to identify critical periods of the breeding cycle of Adélie penguins (*Pygoscelis adeliae*) when the reproductive success may decrease because of instrumentation. For this purpose, we monitored 40 pairs, where one parent was instrumented before egg laying and 30 pairs without devices (controls). These pairs were followed at least during the incubation period but the majority was monitored during the entire breeding season. Reproductive success was affected in pairs where males were instrumented. This was not due to extra chick mortality during chick rearing but to a significantly lower hatching success. Moreover, the use of artificial eggs recording incubation temperatures and egg rotation indicated that in instrumented incubating males, eggs spent as much time at optimal incubation temperatures as control eggs but were rotated at a higher frequency. In Adélie penguins, males initiate incubation and it has been established that the early stage of incubation is one of the most critical periods for embryonic development. The low hatching rate observed in instrumented males was associated with a higher egg rotation rate, perhaps as a stress response to the presence of the instrument. Even though the causal effects remain unclear, instrumentation severely affected hatching success. For these reasons, we recommend equipping birds after the early incubation.

Keywords Incubation · Instrumentation · Penguin · Hatching success

Introduction

Data loggers provide useful information about the behaviour and the physiology of free-ranging animals. However, the main concern for the biologist who uses such instruments should ensure that recorded data are not influenced by biases due to instrumentation itself (Hawkins 2004; Wilson and McMahon 2006).

Among biologging studies, investigations on diving animals are the most represented presumably because biologging finds its origins in the marine environment (Ropert-Coudert et al. 2009). In addition, among diving animals, penguins are over-represented presumably because they are easily accessible, have a large body size and are found in large numbers (Ropert-Coudert et al. 2009). Most studies dealing with the impact of instrumentation in diving animals have naturally focused on deleterious consequences at sea. External devices, such as time–depth recorders or satellite devices, have been described as modifying diving behaviour (Ropert-Coudert et al. 2000, 2006, 2007; Elliott et al. 2007), increasing foraging trip duration (Wanless et al. 1988; Croll et al. 1991; Taylor et al. 2001) and decreasing provisioning rate (Watanuki et al. 1992). These effects were attributed to an additional drag which consequently increased energy expenditure (Culik and Wilson 1991; Bannasch et al. 1994). Moreover, instrumentation has also been reported to modify the behaviour on land of

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birds who try to get rid of the device, preen more frequently and peck the device (Wilson and Wilson 1989; Simeone et al. 2002).

Even though most studies focused on the consequences in instrumented adults, it has been reported that, in seabirds, instrumentation may also indirectly affect reproductive success (Watanuki et al. 1992; Ackerman et al. 2004; Whidden et al. 2007). Three non-exclusive hypotheses can be proposed to explain this lower reproductive success in instrumented seabirds: (1) lower clutch size, (2) lower hatching success, (3) higher chick mortality during chick rearing.

In wild birds, clutch size has been related to the energetic condition of the female during egg formation (Houston 1997; Clifford and Anderson 2001). Consequently, instruments may affect the number of eggs laid only if female birds are equipped before or during egg formation and if instruments prevent them from feeding efficiently. However, birds are usually equipped while they are nesting so that instrumentation never occurs before egg formation which starts before the females reach their breeding sites (Astheimer and Grau 1985).

In contrast, birds may be equipped just before or during incubation (Massey et al. 1988; Ackerman et al. 2004; Whidden et al. 2007) to anticipate the departure of the bird before its first foraging trip. Incubation is a very sensitive period when suboptimal conditions can negatively affect embryonic development. Three main parameters affect the development of the avian embryo: (1) the incubation temperature (Webb 1987), (2) the hygrometric environment of the egg (Bruzual et al. 2000; Snyder and Birchard 2005) and (3) the egg rotations (Van Schalkwyk et al. 2000; Elibol and Brake 2004). In most penguin species, adults can adopt two positions while incubating: the prone and the upright positions. In 1977, Derksen showed that the latter position was associated with egg chilling. Yet, it precisely corresponds to the position that penguins adopt when they preen and particularly when they are instrumented (Wilson and Wilson 1989; Simeone et al. 2002). Consequently, it may be expected that eggs are incubated in non-optimal conditions by instrumented parents if they preen more, resulting in a potential lower hatching success.

Finally, the lower reproductive success observed in instrumented seabirds may be related to increased chick mortality during chick rearing, mainly due to nest abandonment by instrumented adults (Croll et al. 1996; Elliott et al. 2007) and to a decrease in foraging effort and investment for young (Watanuki et al. 1992).

In this study, we examined whether instrumentation affected reproductive success in Adélie penguins (*Pygoscelis adeliae*) equipped before egg laying and throughout the breeding cycle, to highlight the critical periods when the reproductive success may drop off because of instrumentation.

Materials and methods

The study took place in the French polar station Dumont d'Urville (66°40S, 140°00E), Adélie Land, Antarctica during three consecutive austral summers (2006–2007 to 2008–2009).

Study species

In Adélie Land, Adélie penguins breed during the short austral summer from late October to early March. The female lays one or two eggs in mid-November. After clutch completion and the departure of the female at sea to refeed, the male starts to incubate the egg(s) (Derksen 1977). About 12 days later, the female takes the second incubation shift for the same duration. Incubation lasts for on average of 34 days. During the guard stage, both parents each in turn forage at sea to feed and to bring food back to the chick(s) while the other parent protects the chick(s) on the nest. Chicks are left alone when they are 3 to 4 weeks old and are irregularly fed by both parents during the crèche stage (3–4 weeks). Chicks fledge when they are 6 to 8 weeks old (see Ainley 2002 for further details on the breeding chronology of Adélie penguins).

Equipment and monitoring

Reproductive success

At the end of the courtship period, one adult per pair was equipped with a dummy Plexiglas device that mimicked time–depth recorders or satellite devices commonly used in seabirds. The dummy devices were attached to feathers with mastic, cyanoacrylate glue, Tesa tape and cable ties to the middle-back of birds. They were cuboid (2.5 × 3.5 × 6.0 cm) and weighed 60 g; this size was comparable to the size of real devices used in the past with Adélie penguins (Wilson and Wilson 1989; Culik and Wilson 1991, 1992; Watanuki et al. 1992; Miller and Davis 1993). Equipped penguins were then identified with a Nyanzol-D mark painted on the breast feathers, to be visually recognised during the breeding cycle. To minimise the stress of birds, their head was covered by a hood (Cockrem et al. 2008) and the procedure was carried out in ~10 min.

Birds were released close to their nest and the partners of the instrumented birds were captured and identified 2 days later to minimise disturbance due to consecutive captures on the same nest. The identification of the partners helped us to monitor the nests throughout the breeding cycle (location of the nests in the colony, copulations, incubation routine).

In 2006, the experimental group comprised 46 pairs: 16 pairs were assigned in the control group and 30 in the treated group. Treated pairs consisted of an instrumented bird and its untreated partner. In 2008–2009, this group was completed with 24 other pairs: 14 control pairs and 10 pairs where the male was equipped according to the same procedure as in 2006–2007. These birds were only followed during the incubation period to examine their hatching success. In 2006–2007, dummy devices were left on the birds until the moult, at the end of the austral summer, when the device fell off with the feathers to which it was attached. In 2008–2009, dummy devices were removed at the end of the incubation period.

Control and instrumented nests came from the same colony and were randomly selected among the 200 pairs of this colony and equally distributed within the colony. For the breeding cycle in 2006–2007 and during the incubation period in 2008–2009, the nests were observed every 2 h for periods ranging from a few minutes to 2 h to monitor copulation behaviours, laying, hatching and nest reliefs between both partners. The nests were observed with 8 × 20 binoculars from a blind overhanging the subcolony about 20 m away so that we can confidently assume that birds did not notice the presence of the observers.

To determine the sex of the penguins, we used a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962; Kerry et al. 1993). This enabled us to determine that in 2006–2007, among the 30 treated pairs, 13 females and 17 males were instrumented. In 2008–2009, only males were instrumented.

Incubation behaviour

To examine incubation behaviour, another group of penguins was monitored during courtship in 2007–2008 and 2008–2009. This group comprised nine control pairs (four in 2007–2008 and five in 2008–2009) and nine pairs in which the male was instrumented with the same dummy devices as in 2006–2007 (four in 2007–2008 and five in 2008–2009).

Eggs were replaced by untethered artificial eggs as soon as the female left the colony after clutch completion. Artificial eggs have been previously and successfully used in birds including penguins, to monitor a large variety of parameters (Nimon et al. 1996; Giese et al. 1999; Groscolas et al. 2000; Holmes et al. 2005; de Villiers et al. 2006; Becker et al. 2006; Ellenberg et al. 2006). In our study, artificial eggs were the same size as natural eggs, they were filled with Vaseline oil to approach thermal properties of egg content (Coimbra et al. 2006) and the shell was made of white plastic to mimic the colour of natural eggs. Artificial eggs were produced in the IPHC-DEPE (France). They recorded temperatures via six equidistant protruding surface probes around the mid-shell and a probe located in the middle of the egg. Surface probes responded in less than 1 s to a temperature change while the internal probe needed ~20 min to reach the temperature plateau because of the thermal inertia of the egg. The resolution was 0.1°C and the coefficient of variation was 1.3 ± 0.5% (mean ± SD, $N = 8$ eggs) between the six different probes of one egg and 1% between the different eggs (calculated on the mean temperature recorded by all the probes of each egg, $N = 8$ eggs). Egg rotation was also recorded via a 2-axes accelerometer. Each parameter was recorded every 10 s. Artificial eggs were left on the nest during the male and the female first incubation shifts. Meanwhile, natural eggs were artificially incubated in the laboratory (temperature: 32°C, rotation: 180° every 4 h along the long axis). After the female was relieved by her partner, they were replaced in the nest and data from artificial eggs were downloaded onto a computer.

Data analysis

Laying success was defined as the number of laid eggs per pair and hatching success was defined as the number of eggs that hatch per pair. Because it is very difficult to keep track of chicks from particular nests once they have crèched, the final reproductive success was approximated by the number of chicks entering the crèche stage, chick mortality being very rare at this stage (Davis and McCaffrey 1986; Clarke et al. 2002). Incubation duration was considered as the time between the female departure after clutch completion (Derksen 1977) and the first hatching.

To analyse thermal conditions recorded by artificial eggs, we used the maximal temperature recorded by the surface probe in contact with the brood patch and the temperature recorded in the middle of the egg. To better approach the temperature experienced by the embryo, we averaged these two temperatures, since the embryo floats on the yolk and is consequently located between the middle and the upper surface of the egg. In Adélie penguins, Weinrich and Baker (1978) reported that a temperature of 30°C inhibited embryonic development but the embryo can develop at higher temperatures. We defined optimal temperatures as temperatures equal to or higher than 32°C. For each artificial egg, we then calculated the percentage of time spent per day at $T \geq 32$°C.

Concerning egg rotation, to our knowledge, the minimal angle permitting optimal hatchability has not been investigated and may differ between bird species. Elibol and Brake (2006) showed that fertile hatchability and embryonic mortality were similar when broiler eggs were rotated with angles of 35° and 90°. The effects of angles lower than 35°

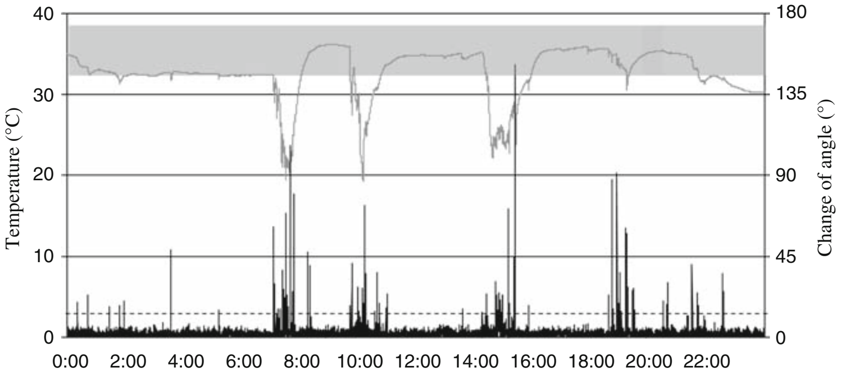

Fig. 1 Example of record by an artificial egg over 24 h at a sampling rate of 10 s. The *grey line* corresponds to the temperature experienced by the embryo (mean of the maximal and the middle temperatures) and the *grey area* represents the range of optimal incubation temperatures (≥32°C). The *black line* corresponds to changes in egg angles between two records and the *dash line* represents the threshold (15°) we used to define the minimal egg rotation

on hatchability have not been investigated. Looking at our results (Fig. 1), angles higher than 15° dissociate distinctly from background noise due to small movements of the incubating bird. This suggests that turning angles of less than 15° were likely attributable to the normal movement of the bird rather than to a specific attempt to actually rotate the egg. For these reasons, we took into account egg rotations with an angle higher than 15° and thus calculated rotation rate per day for each axis. In addition, because the rotation rates per day recorded by the two axes of the accelerometer were very close and highly correlated; we averaged them for statistical analyses.

For statistical analyses, we used a generalised linear model (GzLM) with a Poisson distribution, to compare the number of eggs and chicks between groups [control pairs, pairs with instrumented females (only in 2006–2007) and pairs with instrumented males] considering as fixed factors, the stage (repeated measures: egg laying, hatching, guard stage and crèche stage), the treatment [controls, instrumented-females (only in 2006–2007) and instrumented-males] and the interaction of these two factors. Incubation duration was compared between groups with a general linear model (GLM). To compare the percentage of time spent at optimal incubation temperatures and egg rotation rate (log-transformed to obtain normality) between control and instrumented males, we performed general linear mixed models (GLMM) which allow pseudoreplication to be taken into account by including a random factor (the individual) and a repeated factor (the day of incubation). The group (control or instrumented males) was used as a fixed factor. In addition, since artificial eggs were used in two different years, the year was added to the models as a fixed factor to control for a potential inter-annual variability. Normality of residuals was assessed using a test of Shapiro–Wilk and multiple comparisons were undertaken using the post hoc Bonferroni test.

We used SPSS 16.02 to perform statistical analyses. Results are expressed as means ± SE and significance level was set at $\alpha = 0.05$.

Results

Reproductive success

In 2006–2007, instrumentation significantly affected reproductive success (GzLM: interaction stage*treatment: $\chi^2 = 71.64$, $df = 9$, $P < 0.001$, Fig. 2). The number of laid eggs in control pairs and in pairs with instrumented males was similar (Bonferroni test: $P > 0.99$) but the final reproductive success was 51.5% lower in pairs with instrumented males than in control pairs (Bonferroni test: $P = 0.049$). In pairs with instrumented males, the decrease occurred between laying and hatching since the number of hatched eggs was significantly lower than the number of laid eggs (Bonferroni test: $P < 0.001$). The number of hatched eggs per pair in pairs with instrumented males represented 43.1% of the number of hatched eggs in control pairs (Bonferroni test: $P = 0.003$). This difference between control pairs and pairs with instrumented males remained along the chick-rearing period even though it was not significant in the guard stage (Bonferroni test: $P = 0.07$). After hatching, the number of chicks per pair remained constant until the crèche stage in control pairs (Bonferroni test: $P = 0.46$), pairs with instrumented females (Bonferroni test: $P = 0.30$) and pairs with instrumented males (Bonferroni test: $P > 0.99$). No differences were observed between control pairs and pairs with instrumented females at laying (Bonferroni test: $P > 0.99$), hatching (Bonferroni test: $P > 0.99$), in the guard stage (Bonferroni test: $P > 0.99$) and at the beginning of the crèche stage (Bonferroni test: $P > 0.99$).

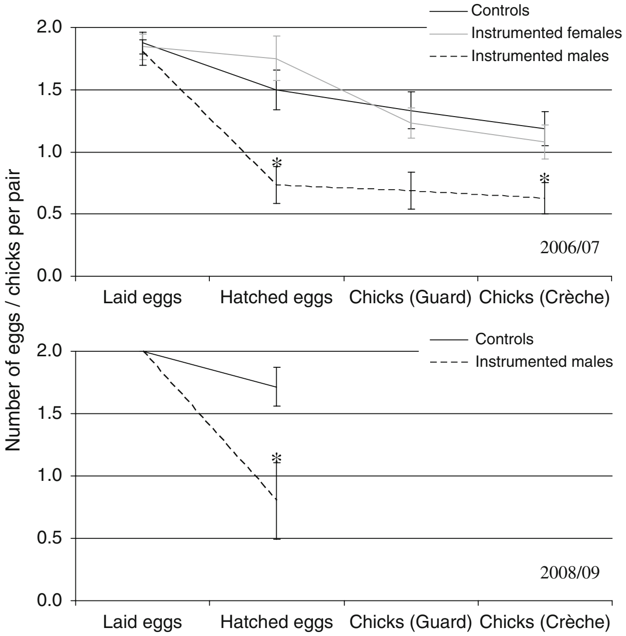

Fig. 2 Number of eggs and chicks per pair in control pairs ($n = 16$ in 2006/2007, $n = 14$ in 2008/2009), instrumented-female pairs ($n = 13$ in 2006/2007) and instrumented-male pairs ($n = 17$ in 2006/2007, $n = 10$ in 2008/2009) throughout the breeding cycle. Results for 2006–2007 are represented in the *top panel* and results for 2008–2009 are represented in the *bottom panel*. Results are presented as mean ± SE. *Asterisk* corresponds to a significant difference ($P < 0.05$) between pairs with instrumented males and control pairs for a given stage

The effect of instrumentation on hatching success observed in 2006–2007 in instrumented males was reproducible since in 2008–2009, instrumentation also significantly decreased hatching success (GzLM: interaction stage*treatment: $\chi^2 = 6.92$, $df = 1$, $P = 0.009$, Fig. 2). While there was no difference in the number of laid eggs (Bonferroni test: $P > 0.99$), hatching success was significantly lower in pairs with instrumented males than in control pairs (Bonferroni test: $P = 0.05$). The number of hatched eggs per pair in pairs with instrumented males represented 47.1% of the number of hatched eggs in control pairs (Fig. 2).

When eggs hatched, incubation duration between control pairs and pairs where males or females were instrumented was similar (31.3 ± 0.4, 31.1 ± 0.4 and 32.1 ± 0.5 days, respectively, GLM: $F_{2,36} = 1.22$, $P = 0.31$).

Incubation behaviour

Incubation parameters differed according to the day of incubation (temperature: $F_{11,156} = 6.34$, $P < 0.001$; rotation rate: $F_{11,156} = 3.12$, $P = 0.001$; Fig. 3). Instrumentation did not have any effect on the time spent at optimal temperatures ($F_{1,16} = 0.22$, $P = 0.65$) but affected the egg rotation rate ($F_{1,16} = 4.94$, $P = 0.04$) with instrumented males turning their eggs more frequently than control males (110 ± 9 and 76 ± 9 egg rotations per day, respectively). The interaction between the animal treatment and the day of incubation was not significant either for temperature ($F_{11,156} = 0.50$, $P = 0.90$) or for egg rotation ($F_{11,156} = 0.91$, $P = 0.53$).

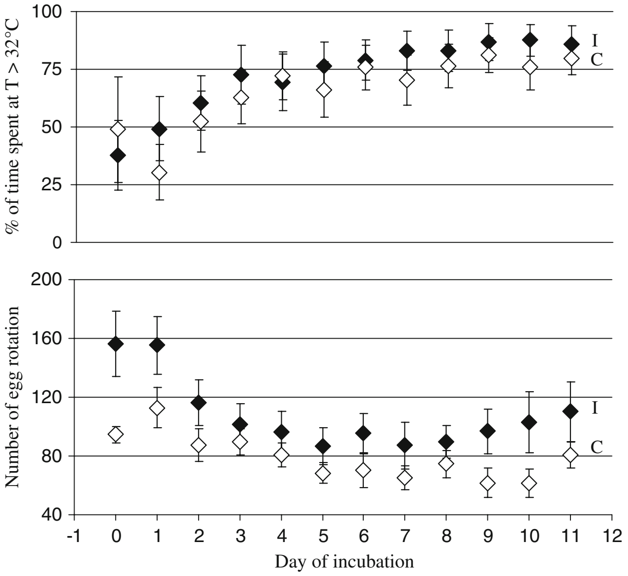

Fig. 3 Percentage of time spent per day at optimal incubation temperatures (≥32°C) and number of egg rotations (>15°) per day of incubation. These data were recorded by artificial eggs placed in the nest of incubating male Adélie penguins. *White symbols* refer to control males (*C* Controls) while *black symbols* correspond to males instrumented with dummy devices (*I* Instrumented). Results are presented as mean ± SE

Discussion

For the first time, this study demonstrates that, in Adélie penguins, instrumentation directly affects reproductive success by decreasing hatching success by nearly half in instrumented-male pairs relative to control pairs, while chick mortality is not increased in instrumented pairs during chick rearing. This suggests that the lower final reproductive success in instrumented penguins does not result from decreased parental care to chicks but from altered incubation behaviour.

Instrumentation has been described as inducing a physiological stress response (Suedkamp Wells et al. 2003) and altered behaviour in birds (Massey et al. 1988; Wilson and Wilson 1989; Simeone et al. 2002). In agreement with these observations, our study highlighted an alteration of the incubation behaviour induced by instrumentation: eggs were incubated in a normal range of temperatures and thus the duration of incubation was not modified, but they were unexpectedly rotated at a higher rate by instrumented males. Therefore, nest attendance, as proxied by the egg temperature, did not appear to be modified in instrumented

Adélie penguins. Moreover, the more frequent manipulation of the egg and the more frequent preening of instrumented penguins as reported by other studies (Wilson and Wilson 1989; Simeone et al. 2002) may be viewed as a derived activity i.e. a contextually functionless behaviour releasing nervousness in a stressful situation (Tinbergen 1952). Nevertheless, the results obtained with the artificial eggs used in our study must be moderated since we cannot rule out that the replacement of the natural clutch (comprising one or two eggs) by one artificial egg may have also generated a stress in incubating birds.

The low hatching success was observed in instrumented males but not in instrumented females. This difference between instrumented males and females is likely to come from the chronology of the breeding cycle of Adélie penguins. As stated before, in this species, males initiate incubation and are in charge of the egg during the first third of the incubation period which precisely corresponds to one of the most critical stage for embryonic development in birds. At this stage, embryos have been described as being very sensitive to hypothermia (Webb 1987), to the absence of egg rotations (Elibol and Brake 2004) or to excessive water loss (Snyder and Birchard 2005). In our study, the lower hatching success associated with a higher rotation rate, may be explained by the erosion of the egg cuticle (Peeble et al. 1987) due to an excessive manipulation of the egg by the instrumented males. Indeed the eggs of Adélie penguins are incubated in a very dry environment. To prevent the eggs from losing too much water, the shell has fewer pores than predicted and is covered by a cuticle during the early part of incubation (Thompson and Goldie 1990). This cuticle disappears as the incubating parents manipulate the egg(s) and is totally absent at the end of incubation thus facilitating respiratory function of the egg. In instrumented males, the rotation rate was so high that it may have eroded the egg cuticle too quickly thus increasing water loss from the egg in the early development of the embryo. It suggests that incubating penguins have to rotate their egg(s) at an optimal rate (~75 times per day in control males), high enough to redistribute heat and nutrients within the egg (Edwards et al. 2003) and to prevent embryo malpositioning (Robertson 1961; Elibol and Brake 2004), but not too high to disrupt the cuticle prematurely. Nevertheless, the hypotheses regarding egg rotation and water loss have to be moderated since incubation parameters and constraints are likely to be different between Adélie penguins and domestic chickens where most incubation parameters have been studied (Peeble et al. 1987; Snyder and Birchard 2005). To confirm this hypothesis, it would be worthwhile incubating penguin eggs subjected to different rotation rates to examine cuticle erosion, water loss and hatching success.

In addition, these deleterious effects during incubation add up to potential negative effects during post-natal chick growth. Chicks coming from instrumented pairs had a lower body mass than control chicks during the guard stage because of a lower provisioning rate (Beaulieu et al. 2009). Further, chicks from pairs with instrumented males were smaller than chicks from pairs with instrumented females (Beaulieu et al. 2009). This may be due to previous abnormal incubation conditions observed in incubating instrumented males. Indeed, even though most studies have looked at developmental condition after hatching, it has been shown that pre-hatching stress has an effect on competitive ability and time spent feeding (Janczak et al. 2007) and abnormal incubation conditions may negatively affect post-hatch growth (Sockman and Schwabl 1998; Metcalfe and Monaghan 2001). Deleterious effects of adult instrumentation are consequently quantitative before hatching (with fewer chicks in pairs with instrumented males) and qualitative after hatching (with smaller chicks in instrumented pairs).

Retrospectively, we tried to confirm whether our results were consistent with those of previous studies. We found eleven articles in which it was possible to determine the time of instrumentation of birds and their reproductive success (Massey et al. 1988; Wanless et al. 1988; Watanuki et al. 1992; Croll et al. 1996; Ballard et al. 2001; Taylor et al. 2001; Watanuki et al. 2003; Ackerman et al. 2004; Hamel et al. 2004; Elliott et al. 2007; Whidden et al. 2007). Birds instrumented while incubating generally exhibited a lower reproductive success (Ackerman et al. 2004; Whidden et al. 2007). However, when instrumentation occured during the final third of incubation, no obvious effects of instrumentation on hatching success were apparent (Massey et al. 1988). Finally, when birds were instrumented at the chick-stage, no deleterious effects of instrumentation on reproductive success were generally reported (Wanless et al. 1988; Ballard et al. 2001; Watanuki et al. 2003; Hamel et al. 2004). However, nest desertion may happen at the chick stage (Taylor et al. 2001; Elliott et al. 2007) resulting in a lower chick survival (Watanuki et al. 1992; Croll et al. 1996). In conclusion, despite the variable responses of species and individuals to instrumentation (Massey et al. 1988), the different specific parameters which could affect hatching success (Koenig 1982) and the variable tolerance of chicks towards abnormal incubation parameters (Webb 1987), bibliographic data support our conclusion stating that the early incubation is the most sensitive period to equip birds since, at this stage, instrumentation strongly affects reproductive success and is also likely to negatively influence offspring quality thereafter. For these reasons, we recommend equipping birds with small and streamlined devices (Bannasch et al. 1994) after the critical early incubation period.

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Article 3 : Réponses à la contrainte environnementale

WHEN SEA-ICE CLOCK IS AHEAD OF ADÉLIE PENGUINS' CLOCK

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When sea-ice clock is ahead of Adélie penguins' clock

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Abstract

1. In Polar Regions, the extent and dynamics of sea-ice are changing. This affects the ocean productivity which consecutively impacts plankton communities and polar top predators like penguins. Yet, the underlying behavioural and physiological mechanisms remain poorly understood.

2. Here we monitored the ecophysiological responses of Adélie penguin (*Pygoscelis adeliae*) pairs during two seasons of contrasting timing of sea-ice retreat. Beside classical breeding parameters like foraging trip duration, body mass and reproductive success, we also investigated food-related stress (*via* plasma corticosterone concentration), nutritional state (*via* metabolite levels) and the use of penguins' habitat (*via* blood isotopic values).

3. Body mass and reproductive success remained unchanged but foraging trips were shorter when sea-ice retreated earlier. Constant plasma corticosterone concentrations indicated that none of the feeding conditions resulted in a food-related stress. However metabolite levels were lower when sea-ice retreated early, suggesting that the foraging performance and the quality/quantity of food differed. Indeed isotopic ratios indicated that coastal prey like fish contributed more to the penguins' diet when sea-ice retreated prematurely.

4. The early sea-ice retreat was related to higher chlorophyll concentrations, known to favour krill recruitment. Paradoxically, this was not associated to a higher krill contribution in the penguins' diet. We propose that a shift in the phytoplankton quality (rather than quantity), affecting krill recruitment, forced penguins to switch to more available prey like coastal fish.

5. In some Antarctic regions, sea-ice is retreating earlier and earlier. In the present study, even though the timing of sea-ice retreat and the consecutive ocean productivity differed drastically between the 2 years, Adélie penguins were not severely affected because they were able to adjust their at-sea behaviour and thus maintained their body condition and reproductive success unchanged.

6. This suggests that the timing of sea-ice retreat does not represent an important threat to populations of Adélie penguins at least as long as alternative resources are still available and other environmental parameters like winter sea-ice extent are not dramatically altered.

Key-words: food availability, krill, phytoplankton, seabird, sea-ice retreat

Introduction

From a predator's perspective, the quality of a particular habitat can be considered as the matching between its requirements and the food available in terms of timing, abundance and accessibility (Durant *et al.* 2007). When the breeding season is conditioned by resource availability, several alternatives are possible for potential breeders when a decrease in food resources happens: animals may (1) skip one breeding season (Drent & Daan 1980), (2) breed but shift their breeding timing according to food availability (Barbraud & Weimerskirch 2006), (3) breed without altering their breeding phenology but mismatch the peak of food availability. In this latter case, animals may change their foraging behaviour and shift to other preys to cope with the lower availability of their usual food resource (Croxall, Reid & Prince 1999; Miller & Trivelpiece 2008; Nicol *et al.* 2008).

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Fig. 1. Adélie penguins on sea-ice edge. Photo by Michaël Beaulieu©.

Because the quality of the habitat is likely to induce effects on the animal physiology and behaviour, the examination of the adequacy between food availability and the animal requirements can be carried out by the investigation of its manifestations on the animal itself. For instance, corticosterone levels have been proposed as a reliable measure of food-related stress and as a consequence a direct measure of food availability in free-living birds (Kitaysky, Piatt & Wingfield 2007). This stress hormone plays an important role in the regulation of feeding, locomotor activity and energy metabolism (see Landys, Ramenofsky & Wingfield 2006) and may affect foraging decisions (Angelier *et al.* 2008). Similarly, plasma metabolite levels highly depend on food intake and can be used as indicators of the nutritional state of free-living animals (Jenni-Eiermann & Jenni 1998). For instance, triglyceride levels reflect the amount of food absorbed and the time since when it was ingested, while uric acid levels characterize protein breakdown which occurs once a critical threshold has been reached in the depletion of body fuel reserves or may result of high muscular activity. Moreover, metabolite levels may also depend on the seasonal requirements of animals; for instance in female birds, before egg laying, triglyceride and uric acid levels reflect the increased liver activity involved in lipid and protein production for oogenesis (Vézina & Williams 2003; Kern *et al.* 2005). Finally a shift in the use of the habitat can be examined by the measurement in animal tissues of stable isotope ratios which indicate simultaneously the trophic position, through $^{15}N : ^{14}N$ ratio (further expressed as $\delta^{15}N$), and the spatial distribution, through $^{13}C : ^{12}C$ ratio (further expressed as $\delta^{13}C$), of the consumer. Indeed, in marine food-webs, low values of $\delta^{15}N$ reflect a diet based on preys found at the bottom of the food-web and high values of $\delta^{13}C$ are found in coastal foragers (for the principle of this measurement, see Inger & Bearhop 2008).

In the Southern Ocean, interactions between algae and krill (mainly *Euphausia superba*) represent the basis for energy flux to higher trophic levels like fish, seabirds and mammals. Krill is essentially herbivorous and grazes on phytoplankton. The intensity of its reproduction is therefore highly correlated with annual primary production in the water column, which in turn depends on sea-ice extent and the timing of its retreat (Quetin & Ross 2001). As a result, the summer krill density and quality (reproductive krill are more energetic) correlate positively with chlorophyll concentrations (Cripps *et al.* 1999; Atkinson *et al.* 2004). In the Arctic, it has been shown that the timing of sea-ice retreat affects the timing of the phytoplankton bloom (Hunt & Stabeno 2002). Indeed sea-ice acts as a physical barrier between the atmosphere and the ocean, preventing daylight from penetrating into the water column. The timing of sea-ice retreat may be variable since sea-ice is relatively thin and is therefore vulnerable to perturbations from the ocean and the atmosphere. In certain regions of Antarctica, on top of a decrease in its extent (Moline *et al.* 2008), sea-ice is also forming ~55 days later and retreating ~30 days earlier than 40 years ago (Stammerjohn *et al.* 2008). As a result, these premature retreats are likely to modify the timing and the intensity of the spring phytoplankton bloom (Moline *et al.* 2008) which by a cascade effect may affect the whole food-web structure.

In this study, we focused on two successive austral summers in Adélie Land which presented contrasting conditions in sea-ice retreat and therefore followed the general trend observed in some Antarctic regions. In 2006–2007, fast sea-ice retreated in late September consecutively to a strong windstorm while in 2007–2008, it retreated, more typically, 3 months later in late December (Fig. 2). This difference of timing was likely to induce consequences on the subsequent phytoplankton bloom, krill and krill-eating predators. Here we examined the link between habitat quality in terms of timing and abundance of phytoplankton and the reproductive and ecophysiological responses of Adélie penguins (*Pygoscelis adeliae*, Fig. 1). During the breeding season in Adélie Land, Adélie penguins principally feed upon krill *Euphausia superba*. However they are not krill-specialists since they can also feed upon Antarctic fish (*Pleuragramma antarcticum*, Ridoux & Offredo 1989; Clarke *et al.* 1998; Wienecke *et al.* 2000). Adélie penguins present a high degree of seasonality: in Adélie Land, they arrive on the breeding grounds in mid-October, lay 1–2 egg(s) in mid-November that hatch in mid-December, chicks are then guarded until mid-January and left in crèches until mid-February (Fig. 3). Food requirement peaks during the chick-rearing period (guard and crèche stages, Chappell *et al.* 1993) when parents have to feed their growing chick(s) and insure their own maintenance. In addition, Adélie pen-

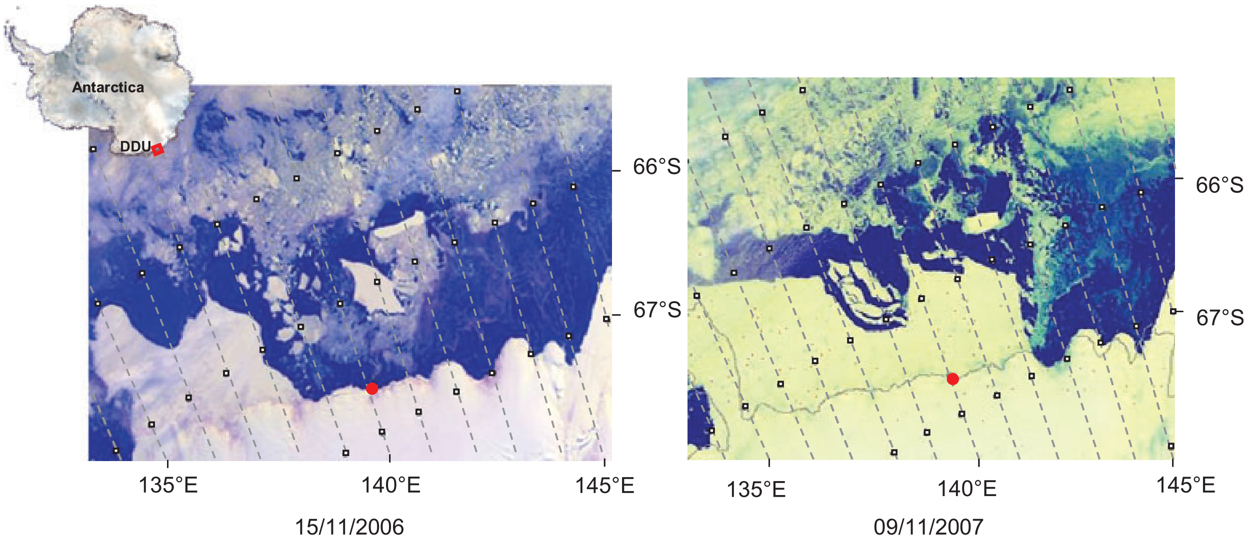

Fig. 2. Satellite images showing sea-ice conditions in Adélie Land in November 2006 and November 2007. Open water areas are represented in blue while ice is represented in white (2006) or yellow (2007). Dumont d'Urville Station (DDU), located on the coast, is symbolized by a red circle. These images were provided by Météo France.

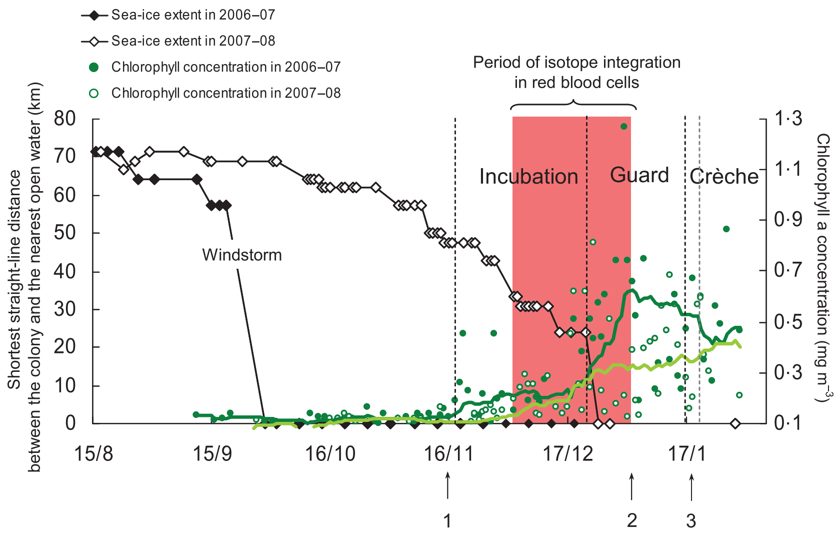

Fig. 3. Evolution of the shortest distance from the colony to the nearest open water due to fast-ice retreat (2006–2007: black symbols, 2007–2008: white symbols) and the consecutive chlorophyll concentration in open water (2006–2007: green-filled symbols, 2007–2008: green-unfilled symbols) from 15 August to 31 January. The moving averages of chlorophyll concentration are represented to facilitate the visualization of its evolution (2006–2007: dark-green line, 2007–2008: light-green line). The breeding phenology of Adélie penguins is superimposed: the limits between two stages were the same in 2006–2007 and 2007–2008 except the limit between the guard and the crèche stages which tended to differ – although non significantly –between the 2 years (2006–2007: black-dashed line, 2007–2008: grey-dashed line). Penguins were weighed and bled twice (arrows 1 and 2) and chicks were weighed at the end of the guard stage (arrow 3). The red area represents the period of isotope integration in red blood cells for the second blood sample.

guins are forced to forage in a limited area (30–110 km from the colony, Angelier *et al.* 2008) because of the constraint to feed chicks regularly. Since sea-ice retreat was premature in 2006–2007, a mismatch between phytoplankton bloom (and presumably krill recruitment) and the requirements of Adélie penguins was likely to happen. In our study, we examined whether differences in the timing of sea-ice retreat affected the timing and/or the abundance of phytoplankton and to what extent it may have affected Adélie penguins' body condition, metabolisms of lipids and proteins, foraging decisions, diet quality and ultimately breeding success.

Materials and methods

FIELD PROCEDURE

In 2006–2007, at the end of the courtship period, 32 birds from 16 different pairs from Dumont d'Urville, Pétrel Island (66°40′S, 140°01′E;

Fig. 2), were captured on their nest and weighed with an electronic balance (Ohaus, ± 2 g). The birds were then identified with a Nyanzol-D mark painted on the breast feathers and with a subcutaneous passive transponder (Renner & Davis 2000). To minimize disturbance due to consecutive captures on the same nest, the partner underwent a similar treatment 2 days later.

Until the end of the guard stage, the 16 nests were observed from a blind overhanging the nests, about 20 m apart, every 2 h at worst and continuously at best to monitor copulation behaviours, laying, foraging trip duration and reproductive success. Laying date was defined as the laying date of the first egg. Provisioning rate was defined from the chick perspective and was calculated as the number of parent returns (male + female) from the sea during the guard stage. The number of chicks in crèche was used to estimate the final reproductive success of the focal pairs since at this stage, chick mortality is low in Adélie penguins (Davis & McCaffrey 1986; Clarke *et al.* 2002).

The birds were captured and weighed a second time during the guard stage (40–45 days after laying), after a nest relief and just before leaving the colony to forage at sea (Fig. 3). Body mass loss was defined as the difference between the first and the second weighing.

Blood was collected during the two captures (courtship and guard stage, Fig. 3) from the wing vein with a heparinized syringe. After centrifugation, plasma and red blood cells were quickly stored at −20 °C. Because the capture and the restraint constitute an acute stress that may influence baseline parameters in blood (Jenni-Eiermann & Jenni 1998; Cockrem *et al.* 2008), most attention was paid to minimize the stress for birds. The head of the penguin was covered by a hood (Cockrem *et al.* 2008) and handling duration was minimized and timed from the approach of the experimenter towards the nest until the end of blood sampling. A 5-min threshold was chosen since it has been shown that handling durations < 5 min had no effect on corticosterone levels in Adélie penguins (Vleck *et al.* 2000). Timing of blood sampling depended on the bird departure and therefore occurred at any time of the day. However corticosterone concentration is not affected by daytime in Adélie penguins (Vleck & Van Hook 2002, Angelier *et al.* 2008).

At the end of the guard stage, the chicks were weighed on their nest with a spring balance (Salter, ± 20 g) when they were left unguarded for the first time.

In 2007–2008, at the end of the courtship period and twice during the incubation period, all the nests occupied by pairs in 2006–2007 were checked with a hand held antenna to search for penguins identified with transponders. For the rest of the breeding cycle, the procedure was strictly the same as that described in 2006–2007.

In both years, adults were sexed by a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962; Kerry, Clarke & Else 1993). Sex determination carried out in 2007–2008 totally confirmed the sexing of all birds achieved 1 year before.

LABORATORY ANALYSES

Analyses of the plasma concentrations of corticosterone, triglycerides and uric acid were conducted at the IPHC-DEPE, France. Corticosterone levels were determined by immunoassay (AssayMax Corticosterone ELISA Kit; AssayPro, St. Charles, Missouri, US) and concentrations of triglycerides and uric acid were measured using enzymatic colorimetric tests (Sigma Diagnostic, St. Louis, Missouri, US). Intra- and inter- assay variations were 5% and 7%, respectively for corticosterone measurements and were comprised between 1% and 3% for metabolite measurements. In addition, the cross-reactivity of the corticosterone antibody with other steroids is low (comprised between 0 and 2%, Assay Pro). No relationship between handling time and corticosterone levels was found (courtship 2006: $r_s = 0{\cdot}04$, $P = 0{\cdot}86$; courtship 2007: $r_s = -0{\cdot}26$, $P = 0{\cdot}29$; guard stage 2006–2007: $r_s = -0{\cdot}03$ $P = 0{\cdot}91$; guard stage 2007–2008: $r_s = -0{\cdot}20$ $P = 0{\cdot}41$), so that we considered these corticosterone levels reflected baseline values.

Tissue isotopic values mirror the diet throughout the period of tissue synthesis (Bearhop *et al.* 2002). We chose to investigate isotopic values of red blood cells, which require 3–4 weeks to turn-over (Hobson & Clark 1993; Haramis *et al.* 2001; Bearhop *et al.* 2002) and thus integrated the diet of the bird from the end of the incubation period to the early guard stage (second blood sample, Fig. 3). Before isotopic analyses, red blood cells were lyophilized (48 h) and powdered (Hobson, Gibbs & Gloutney 1997). Lipids were not extracted as this is not necessary when using red blood cells (Cherel *et al.* 2005). Stable-carbon and nitrogen isotope assays were carried out at the Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA), L'Houmeau, France. Results are expressed in the standard δ notation (‰) relative to PDB belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Intra-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0·88% and 0·63%, respectively. Inter-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0·42% and 0·24%, respectively.

ENVIRONMENTAL ANALYSIS

In both years, we measured the shortest straight-line distance between the colony and the nearest open water on cloud-free satellite images (resolution: 1 km) provided by Météo France. To measure chlorophyll concentration, we used SEAWIFS satellite data (NASA-OrbImage, resolution: 1 km) that provided mean chlorophyll *a* concentration in open-water areas in a region that extended latitudinally from 65°00′S to 66°40′S and longitudinally from 135°00′E to 145°00′E (Fig. 2). Since chlorophyll concentration varies as a function of daytime (McMinn *et al.* 2007), it was measured only between 13:00 and 15:00 local time. Environmental data were analysed from 15 August to 31 January.

DATA ANALYSIS

A population is characterized by diversity and variance as it is composed of animals of different age, experience, quality etc. In order to perform inter-annual comparisons and avoid confounding factors due to inter-individual variability, two alternate sampling protocols are conceivable: (1) sample each year a large number of individuals equally sampling all the categories found in the population (or even better in the species) or (2) repeatedly sample each year the same number of animals so that the experimenter is sure that the confounding factors due to sampling are the same year after year. As the first alternative is logistically too difficult, we chose the second option thus assuming that the potential inter-individual confounding factors were the same each year. Since newly-established pairs have a lower breeding success in Adélie penguins (Ainley, Leresche & Sladen 1983) and that a change of mate may increase corticosterone levels (Angelier *et al.* 2007), we removed the potential bias due to pair stability by considering only stable pairs from 2006–2007 to 2007–2008. This resulted in the exclusion of five pairs that divorced or in which one mate was absent in 2007–2008. Moreover, because metabolic levels do not lead to the same interpretation during incubation and chick-rearing periods (see introduction) and corticosterone levels may also change within a breeding season (Lanctot *et al.* 2003), we conducted comparisons between the 2 years during the incubation period and during the guard stage independently.

The concentrations of chlorophyll were compared between the 2 years after the chlorophyll bloom (15 November) with a Mann–Whitney test. Using the date of laying as the reference date, we assessed with general linear models whether the dates of manipulation and sampling differed between the 2 years. Almost all other comparisons were carried out using general linear mixed models to avoid the problem of pseudoreplication since our statistical analyses involved repeated observations of the same subjects. Individuals were considered as a random factor while the year, the sex and their interaction were used as fixed factors. Normality of residuals was assessed by Shapiro-Wilk tests. When this condition was not fulfilled, we used generalized linear models with a normal distribution (duration of the first foraging trip during incubation) or a gamma distribution of dependent data (plasmatic parameters, foraging trip duration during the guard stage). Generalized linear models with a Poisson distribution were also used in the case of count data (reproductive success) considering the stage (egg laying, hatching, guard stage and crèche stage), the year and the interaction of these two factors as fixed factors. Multiple comparisons were undertaken using the post hoc Bonferroni test.

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL, USA). Results are expressed as means ± SE and significance level was set at $\alpha = 0·05$.

Results

ENVIRONMENTAL PARAMETERS

The distance from the colony to the nearest open water was similar (70 km) in mid-August 2006 and 2007. In 2006–2007, open water reached the coast of the colony 3 months before it did in 2007–2008 (Fig. 3). Chlorophyll concentrations began to increase at the same time in both years (15 November). After this date, chlorophyll mean concentration was 30% lower in 2007–2008 ($0·287 \pm 0·024$ mg m^{-3}) than in 2006–2007 ($0·404 \pm 0·035$ mg m^{-3}, $U = 880$, $P = 0·006$, Fig. 3).

PRE-LAYING PERIOD

There was no difference in the handling date between the 2 years ($F_{1,\,39} = 1·05$, $P = 0·31$) and females and males were manipulated at the same time ($F_{1,\,39} = 3·29$, $P = 0·08$). The interaction year × sex was not significant ($F_{1,\,39} = 2·28$, $P = 0·14$, Table 1).

Before egg laying, males were heavier than females ($5·12 \pm 0·10$ and $4·53 \pm 0·10$ kg, respectively; $F_{1,\,38} = 18·12$, $P < 0·001$) but neither the year ($4·83 \pm 0·10$ kg in 2006 and $4·82 \pm 0·10$ kg in 2007, $F_{1,\,38} = 0·01$, $P = 0·94$) nor the interaction sex × year ($F_{1,\,38} = 0·74$, $P = 0·40$) had an effect on body mass (Fig. 4).

Concentrations of corticosterone were similar between males and females ($2·32 \pm 0·51$ and $1·86 \pm 0·53$ ng mL^{-1}, respectively; Wald $\chi^2 = 0·39$, d.f. = 1, $P = 0·53$) and between years ($1·92 \pm 0·46$ in 2006 and $2·26 \pm 0·45$ ng mL^{-1} in 2007, Wald $\chi^2 = 0·40$, d.f. = 1, $P = 0·53$). The interaction sex × year was also not significant (Wald $\chi^2 = 1·83$, d.f. = 1, $P = 0·18$, Fig. 4).

Plasma concentrations of uric acid and triglycerides followed the same trends: metabolite concentrations were lower in males than in females (uric acid: $0·21 \pm 0·01$ and $1·16 \pm 0·08$ mmol L^{-1}, respectively; Wald $\chi^2 = 9·88$, d.f. = 1, $P = 0·002$, triglycerides: $1·33 \pm 0·12$ and $10·96 \pm 1·26$ mmol L^{-1}, respectively; Wald $\chi^2 = 58·21$, d.f. = 1, $P < 0·001$) and there were differences between years (uric acid: $0·60 \pm 0·04$ in 2006–2007 and $0·77 \pm 0·05$ mmol L^{-1} in 2007–2008, Wald $\chi^2 = 15·46$, d.f. = 1, $P < 0·001$, triglycerides: $3·09 \pm 0·73$ in 2006–2007 and $9·20 \pm 0·78$ mmol L^{-1} in 2007–2008, Wald $\chi^2 = 54·51$, d.f. = 1, $P < 0·001$). The interaction sex × year (uric acid: Wald $\chi^2 = 9·88$, d.f. = 1, $P = 0·002$, triglycerides: Wald $\chi^2 = 48·74$, d.f. = 1, $P < 0·001$) indicated that metabolite concentrations remained stable in males (uric acid: $P = 0·79$, triglycerides: $P = 0·13$) while they increased between 2006–2007 and 2007–2008 in females (uric acid: $P = 0·001$, triglycerides: $P < 0·001$, Fig. 4).

INCUBATION PERIOD

There was no difference in the laying date between both years ($F_{1,\,9} = 0·02$, $P = 0·90$, Table 1). The first foraging trip was longer in 2007–2008 than in 2006–2007 ($13·47 \pm 0·32$ and $10·83 \pm 0·26$ days, respectively; Wald $\chi^2 = 45·68$, d.f. = 1, $P < 0·001$) but neither the sex (Wald $\chi^2 = 1·64$, d.f. = 1, $P = 0·20$) nor the interaction year × sex affected its duration (Wald $\chi^2 = 0·15$, d.f. = 1, $P = 0·70$, Fig. 4). Egg hatching

Table 1. Principal dates of the breeding cycle of the studied Adélie penguin pairs and dates of handling

	2006–2007		2007–2008	
	Females ($n = 11$)	Males ($n = 11$)	Females ($n = 11$)	Males ($n = 11$)
Duration between the first handling and egg laying (days)	$-5·8 \pm 0·9$	$-2·8 \pm 0·9$	$-5·4 \pm 0·9$	$-5·09 \pm 0·9$
Date of laying	17/11 ± 0·6 days	–	17/11 ± 1·1 days	–
Date of hatching	23/12 ± 0·8 days		23/12 ± 0·8 days	
Duration between egg laying and the second handling (days)	$41·2 \pm 0·6$	$41·3 \pm 0·6$	$40·6 \pm 0·6$	$40·2 \pm 0·6$
Duration of the guard stage (days)	$25·2 \pm 1·5$		$28·7 \pm 1·6$	

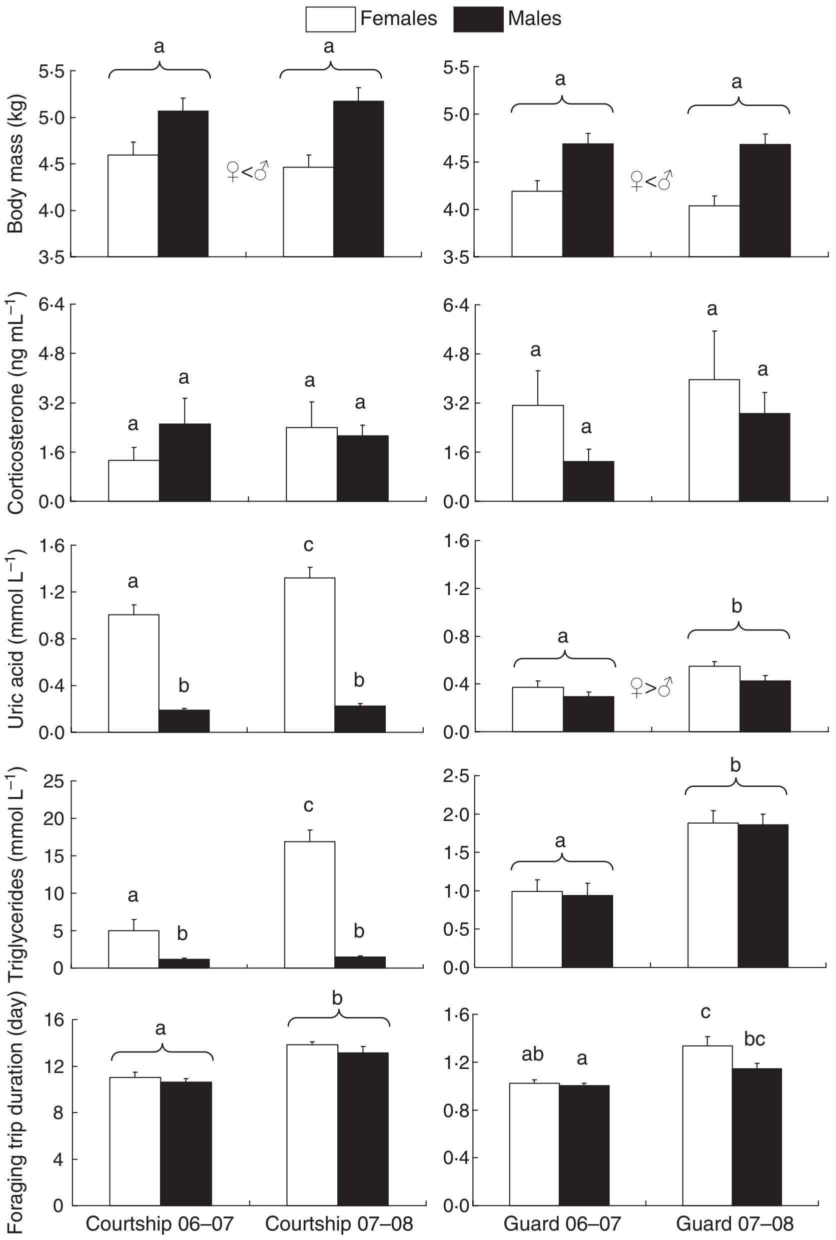

Fig. 4. Body mass, plasmatic parameters (corticosterone, uric acid and triglyceride) and foraging trip duration during the courtship and the incubation periods (left column) and during the guard stage (right column) in 2006–2007 and 2007–2008. White histograms refer to females and black histograms refer to males. Results are presented as means ± SE. Comparisons were carried out during the courtship and the incubation periods and during the guard stage independently. Different letters correspond to significant differences between two groups for a considered parameter and the brackets indicate the results of the comparison between the 2 years whatever the sex of the individuals.

happened at the same date ($F_{1,\,9}$ = 0·03, P = 0·88) in 2006–2007 and in 2007–2008 (Table 1).

GUARD STAGE

There was no difference in the handling date during the guard stage between the 2 years ($F_{1,\,36}$ = 2·13, P = 0·15), between sexes ($F_{1,\,36}$ = 0·04, P = 0·84) and the interaction year × sex was not significant ($F_{1,\,36}$ = 0·16, P = 0·69, Table 1).

Body mass was higher in males than in females (4·69 ± 0·10 and 4·11 ± 0·10 kg, respectively; $F_{1,\,18}$ = 16·08, P = 0·001) but neither the year (4·44 ± 0·08 kg in 2006–2007 and 4·36 ± 0·08 kg in 2007–2008, $F_{1,\,17}$ = 1·73, P = 0·21) nor the interaction sex × year ($F_{1,\,17}$ = 1·57, P = 0·23) influenced body mass (Fig. 4). Body mass changed similarly between the pre-laying period and the guard stage (mean body mass loss: 393 ± 59 g) in both years ($F_{1,\,16}$ = 0·41, P = 0·53) and in males and females ($F_{1,\,17}$ = 1·74, P = 0·21). The interaction sex × year was not significant ($F_{1,\,17}$ = 0·78, P = 0·79).

Corticosterone remained constant between males and females (2·07 ± 0·47 and 3·54 ± 0·82 ng mL^{-1}, respectively; Wald χ^2 = 2·41, d.f. = 1, P = 0·12) and between years (2·21 ± 0·59 in 2006–2007 and 3·40 ± 0·87 ng mL^{-1} in 2007–2008, Wald χ^2 = 1·07, d.f. = 1, P = 0·30). The interaction sex × year was also not significant (Wald χ^2 = 0·10, d.f. = 1, P = 0·75). Metabolite concentrations were higher in 2007–2008 than in 2006–2007 (uric acid: 0·49 ± 0·03 and 0·33 ± 0·03 mmol L^{-1}, respectively, Wald χ^2 = 16·74, d.f. = 1, P < 0·001, triglycerides: 1·87 ± 0·10 and 0·96 ± 0·11 mmol L^{-1}, respectively; Wald χ^2 = 54·42, d.f. = 1, P < 0·001) and sex had only an effect on uric acid concentrations (uric acid: 0·36 ± 0·03 mmol L^{-1} in males and 0·46 ± 0·04 mmol L^{-1} in females, Wald χ^2 = 1·11, d.f. = 1, P = 0·04, triglycerides: 1·40 ± 0·13 mmol L^{-1} in

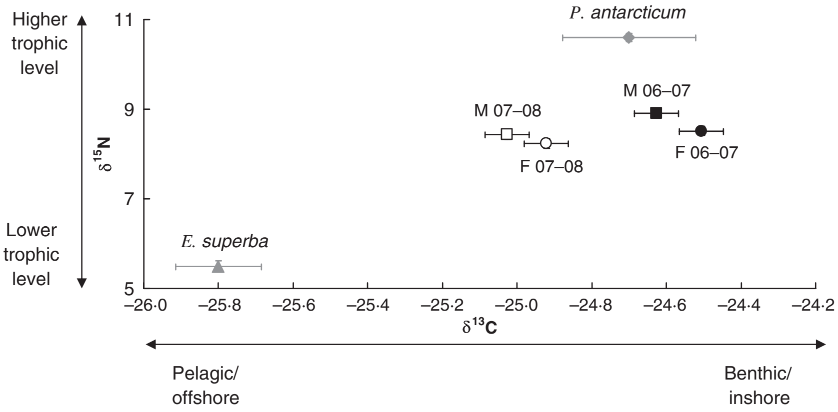

Fig. 5. Mean δ^{15}N and δ^{13}C (±SE) values of adult Adélie penguins, males (squares) and females (circles) in 2006–2007 (filled symbols) and 2007–2008 (empty symbols). Values for *Euphausia superba* and *Pleuragramma antarcticum* are also represented (from Cherel 2008).

males and 1·44 ± 0·12 mmol L^{-1} in females, Wald χ^2 = 0·04, d.f. = 1, *P* = 0·84). The interaction sex × year was not significant neither for uric acid (Wald χ^2 = 0·29, d.f. = 1, *P* = 0·59) nor for triglycerides (Wald χ^2 = 0·01, d.f. = 1, *P* = 0·91, Fig. 4).

During the guard stage, foraging trip duration was affected by the sex (1·07 ± 0·03 days in males and 1·17 ± 0·04 days in females, Wald χ^2 = 4·12, d.f. = 1, *P* = 0·04), the year (1·01 ± 0·02 days in 2006–2007 and 1·24 ± 0·04 days in 2007–2008, Wald χ^2 = 28·03, d.f. = 1, *P* < 0·001) and the interaction sex × year (Wald χ^2 = 3·98, d.f. = 1, *P* = 0·05) with males performing 15% longer foraging trips in 2007–2008 than in 2006–2007 (*P* = 0·001) and females performing 30% longer foraging trips in 2007–2008 than in 2006–2007 (*P* < 0·001, Fig. 4). Over the guard stage, the provisioning rate was similar in 2006–2007 and in 2007–2008 (2006–2007: 22·70 ± 1·54 parent returns, 2007–2008: 20·44 ± 1·63 parent returns, $F_{1,\ 17}$ = 1·01, *P* = 0·33). This was due to the nearly significantly longer guard stage (∼3·5 days) in 2007–2008 than in 2006–2007 ($F_{1,\ 9}$ = 4·14, *P* = 0·07, Table 1), since provisioning rate was significantly different between the 2 years after controlling for the duration of the guard stage (2006–2007: 24·06 ± 0·98 visits, 2007–2008: 18·93 ± 1·04 visits; $F_{1,\ 16}$ = 12·14, *P* = 0·003).

Isotopic values differed according to the sex and the year: males had higher levels of δ^{15}N than females (8·7 ± 0·1 ‰ and 8·4 ± 0·1 ‰, respectively, $F_{1,\ 18}$ = 6·29, *P* = 0·02) but δ^{13}C values were similar in both sexes (males: −24·8 ± 0·1 ‰, females: −24·7 ± 0·1 ‰, $F_{1,\ 18}$ = 2·67, *P* = 0·12). Both δ^{15}N and δ^{13}C values were different between the 2 years with higher δ^{15}N values in 2006–2007 than in 2007–2008 (8·7 ± 0·1 ‰ and 8·3 ± 0·1 ‰, respectively, $F_{1,\ 18}$ = 23·20, *P* < 0·001), associated with higher δ^{13}C values (2006–2007: −24·6 ± 0·1 ‰, 2007–2008: −25·0 ± 0·1 ‰, $F_{1,\ 18}$ = 74·35, *P* < 0·001). The interaction sex × year was not significant neither for δ^{15}N values ($F_{1,\ 18}$ = 1·67, *P* = 0·21) nor for δ^{13}C values ($F_{1,\ 18}$ = 0·03, *P* = 0·87, Fig. 5).

REPRODUCTIVE SUCCESS AND BROOD MASS

Even though the breeding stage had an effect on reproductive success (Wald χ^2 = 35·56, d.f. = 3, *P* < 0·001, Fig. 6), there was no difference between the 2 years (Wald χ^2 = 0·30, d.f. = 1, *P* = 0·59) and the interaction stage × year was not significant (Wald χ^2 = 1·64, d.f. = 3, *P* = 0·65). At the end of the guard stage, brood mass was similar in 2006–2007 and in 2007–2008 (3·01 ± 0·34 kg and 3·02 ± 0·35 kg, respectively, $F_{1,\ 9}$ = 0·00, *P* = 0·98).

Discussion

Few studies have tried to establish a link between ecological, behavioural, dietary and physiological parameters in wild animals. Here, we showed that a 3-months earlier fast-ice retreat was associated to a 30% higher chlorophyll production in open water and it affected Adélie penguins who performed shorter foraging trips, and fed on a diet with higher δ^{15}N and δ^{13}C values. They presented lower plasma metabo-

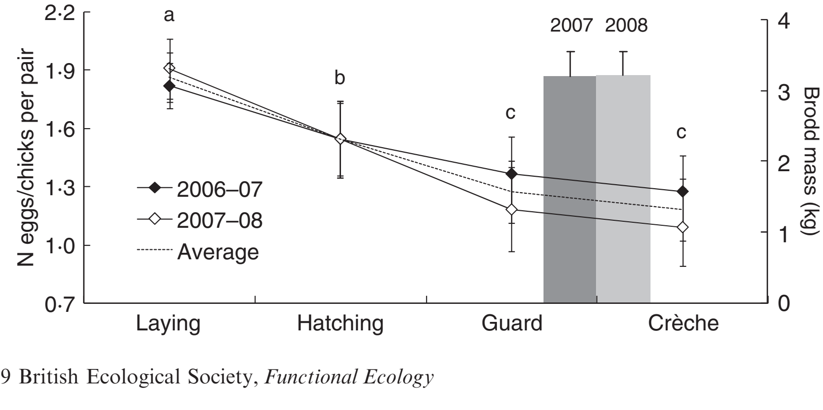

Fig. 6. Reproductive success of Adélie penguin pairs as a function of the number of eggs laid, hatched, the number of chicks during the guard and the crèche stages in 2006–2007 and 2007–2008. Histograms represent brood mass at the end of the guard stage. Results are presented as mean ± SE. Different letters correspond to significant differences between two consecutive stages for the mean reproductive success.

lite levels but corticosterone levels, body mass and reproductive success were not altered.

Interestingly, the early fast sea-ice retreat did not result in a premature phytoplankton bloom as previously described in the Arctic (Hunt & Stabeno 2002). As a result, Adélie penguins, who did not modify their breeding phenology, did not mismatch the peak of primary productivity. This match in timing between phytoplankton bloom and Adélie penguin breeding season occurred probably because both rely on the same environmental cues (i.e. daylight duration and intensity). However the early fast-ice retreat was followed by a 30% higher peak of primary production. In 2006–2007, krill stocks were thus expected to be more abundant and presumably more energetic since the recruitment must have been higher (Cripps *et al.* 1999; Quetin & Ross 2001; Atkinson *et al.* 2004). However, looking at isotopic values, higher values of δ^{15}N indicated that penguins did not feed more at lower trophic levels (krill) than at higher trophic levels (fish) in 2006–2007. This discrepancy between expected krill availability (estimated through chlorophyll concentration) and krill exploitation by Adélie penguins may come from a mismatch between phytoplankton bloom and krill recruitment in 2006–2007. Adult krill is known to feed on the phytoplankton bloom at the ice edge (Nicol 2006). In 2006–2007, as the ice edge had totally disappeared, krill recruitment may have been altered. Indeed it has been shown that an early sea-ice retreat was associated with the dominance of 'small' pico-nano-phytoplankton (<20 μm, cryptophytes) on 'large' micro-phytoplankton (>420 μm, diatoms; Montes-Hugo *et al.* 2008). As a result, even if the overall chlorophyll concentration was higher in 2006–2007 than in 2007–2008, a shift in the size distribution of the phytoplankton community is likely to have occurred, with small phytoplankton prevailing in 2006–2007. As the grazing efficiency of *Euphausia superba* decreases significantly with particles <20 μm (Moline *et al.* 2004), these specific conditions could have led to a lower krill recruitment in 2006–2007 than in 2007–2008. As a result, a high chlorophyll production is not necessarily associated with high krill recruitment. This may explain why, in 2006–2007, Adélie penguins were forced to partially shift to a diet with a higher contribution of fish resulting in higher δ^{15}N plasma values. Ainley *et al.* (2003) also found that Adélie penguins eat more fish in years with less sea-ice in the Ross Sea, suggesting that a low sea-ice cover may increase the relative abundance and/or the accessibility of fish.

As suggested by isotopic values, *Pleuragramma antarcticum* inhabits more coastal areas (higher δ^{13}C values) than *Euphausia superba* (lower δ^{13}C values, Cherel 2008). In agreement with this, isotopic measures showed that penguins fed more on higher trophic levels in coastal areas (higher δ^{15}N and δ^{13}C values) while they fed more on lower trophic levels in pelagic areas (lower δ^{15}N and δ^{13}C values, Fig. 5). Two non-exclusive reasons can explain why penguins fed more predominantly on krill in more pelagic areas in 2007–2008: (1) the presence of the fast-ice forced the penguins to reach the limit ice-edge/open water, 20–30 km away from the colony (Fig. 3), where krill is present (Nicol 2006), (2) Adélie penguins are known to feed preferentially on gravid energetic female krill (Clarke *et al.* 2002; Nicol *et al.* 2008) that live and spawn offshore (Nicol 2006). This may also explain why penguins performed longer foraging trips in 2007–2008, even when fast-ice disappeared during the guard stage.

The absence of changes in body mass and corticosterone levels between the 2 years suggested that none of the environmental conditions in the 2 years induced a food-related stress for birds. The fact that the diet differed between both years does not necessarily mean that 1 year was inferior to the other in terms of food availability. Overall food availability (krill and/or fish) may not have been drastically different and because Adélie penguins are generalist feeders, they were able to adjust their diet to the contrasting environmental conditions. Nevertheless, our results may have been biased by our selective sampling method since only birds remaining in a stable pair and present each year in the colony were included in the analysis; we may have thus selected only the most competitive birds able to respond to different levels of food availability without experiencing any food-related stress.

Metabolite levels were higher in 2007–2008 than in 2006–2007. The diet richer in krill (2007–2008) could be therefore considered as more profitable for birds than the diet richer in fish (2006–2007): as triglyceride and uric acid levels were higher in 2007–2008, one can hypothesize that birds consumed larger amount of food, stored more fat and had a higher-protein diet in 2007–2008 than in 2006–2007. However, body mass was not higher in 2007–2008 than in 2006–2007. Moreover protein content is similar in krill and fish (*Euphausia superba*: 10% of wet weight, *Pleuragramma antarcticum*: 11% of wet weight, Reinhardt & Van Vleet 1986) and lipid content is lower in krill than in fish (*Euphausia superba*: 5% of wet weight, *Pleuragramma antarcticum*: 10% of wet weight; Clarke 1980; Friedrich & Hagen 1994). One alternative explanation could be that krill lipids and proteins may be better assimilated than those of fish. Another way to interpret higher observed uric acid levels in 2007–2008, is that penguins increased protein breakdown by providing a higher muscular effort (Jenni-Eiermann & Jenni 1998) when they foraged on krill in more pelagic areas and during longer foraging trips. In the same line of thought, since foraging trip duration was longer in females than in males, females may have to provide a greater effort than males to obtain the same diet, which may explain why their uric acid levels were higher than those of males.

Comparing our results to other studies dealing with Adélie penguins facing different environmental conditions, it is interesting to notice that all parameters are not similarly modified in all studies (Table 2). The laying date, the laying success or the hatching date did not vary in any study. In contrast, some parameters changed in all studies (foraging trip duration, decreased meal size, duration of the guard stage) and can therefore be considered as sensitive indicators of a modification in the environment of Adélie penguins. Arrival body mass, diet quality, breeding success and fledgling mass varied in some studies but not in others. This is likely to be due to variable differences in food availability between the two

Table 2. Comparison of four studies dealing with consequences of inter-annual environmental conditions and breeding in Adélie penguins

	This study	Clarke *et al.* 2002*	Nicol *et al.* 2008;	Olmastroni *et al.* 2004;	Clarke *et al.* 2002†
Location	Dumont d'Urville	Béchervaise Island	Béchervaise Island	Edmonson Point	Béchervaise Island
Difference in primary production	30%	NI	NI	NI	NI
Difference in krill availability	NI	NI	70%	NI	NI
Decreased arrival body mass	No	No	No	Yes	No
Decreased laying success	No	NI	No	No	NI
Delayed laying	No	No‡	No	No‡	No‡
Delayed hatching	No	NI	No	No	NI
Increased foraging trip duration	F (30%) M (15%)	F (30%) M (20%)	F (50%) M (40%)	NI	F (150%) M (30%)
Change in diet quality	Yes	No	Yes	NI	No
Increased corticosterone levels	No	NI	NI	NI	NI
Different metabolic state	Yes	NI	NI	NI	NI
Decreased meal size	NI	Yes	Yes	NI	Yes
Delayed crèching date	(Yes)	NI	Yes	Yes	NI
Decreased breeding success	No	Yes	Yes	Yes	Yes
Decreased fledgling mass	No	Yes	No	NI	All chicks died

Studies are presented from the left to the right according to the percentage of increased foraging trip duration. Data from Clarke *et al.* (2002) are presented for years 1993–1994 (†) and 1997–1998 (*) and are completed with data provided by Emmerson *et al.* (2003). For some studies, the laying date was approximated by the female departure after egg laying (‡). The increase in foraging trip duration is presented in percentage for females (F) and males (M) during the guard stage. 'Yes' indicates a difference and 'No' indicates no differences between the two considered years (the reference year being that when foraging trips were the shortest). NI indicates that the parameter was not investigated.

considered years. It is also important to note that most studies, like ours, usually consider a limited number of years with different level of food availability and thus do not cover the full spectrum of feeding conditions. Some parameters vary with a small difference between two environmental situations while others vary only if this difference is important. For instance, we did not detect any effect of environmental variability on breeding success while other studies did. It is likely because the birds of our study experienced the smallest modification of their environment compared to other studies. This is in agreement with foraging trip duration which increase was one of the smallest of all studies.

In Béchervaise Island, between 1997 and 1998, foraging trip duration increased similarly as in our study (Clarke *et al.* 2002). However, in contrast to our data, their breeding success decreased the year when penguins foraged for a longer time. This discrepancy may come from the possibility that our penguins had to change the quality of their diet so that they could feed their chicks properly. This shift in diet was not observed in Béchervaise Island between 1997 and 1998, and may explain why breeding success was affected. This hypothesis is reinforced by Nicol *et al.* (2008): in their study, even though foraging trip duration increased more importantly than in our study, breeding success remained unchanged. Birds may have been able to maintain their breeding success because, like in our study, they were able to modify their diet.

Our study is a first attempt to relate environmental conditions to behavioural, dietary, breeding and physiological parameters in Adélie penguins. This approach is promising but proved to be an uneasy task because it integrates many levels (sea-ice, phytoplankton, krill, fish, penguins' behaviour and physiology). Consequently results are sometimes difficult to interpret. Unfortunately we were not able to compare our physiological data to other data since no other studies, examining the effects of contrasting environmental conditions on Antarctic top predators, investigated the animals' physiology (Table 2). In the other studies dealing with Adélie penguins, birds appeared to have experienced more severe modifications of their environment so that their physiological response is likely to have been different to that in our study. In addition, we have considered the isotopic values of prey as constant over time while they may also have fluctuated between years. To better understand the underlying mechanisms between environmental constraints and ecophysiological responses of Antarctic top predators, further studies should integrate data on animals' behaviour, prey, endocrinology and physiological state over a large spectrum of environmental conditions.

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Article 4 : Comportement de plongée associé aux deux contraintes

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DIVING ADAPTABILITY OF ADÉLIE PENGUINS WITH DIFFERENT DIVING CAPACITIES, IN RESPONSE TO ENVIRONMENTAL CONSTRAINTS

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(en préparation)

ABSTRACT

Foraging behaviour is modulated by environmental and individual characteristics. Therefore, individuals are supposed to differ in their capacity to adapt to environmental changes.

We experimentally mimicked low diving capacities in Adélie penguins (*Pygoscelis adeliae*) by attaching them large dummy devices associated with a smaller time-depth recorder. Their diving behaviour was compared to that of penguins equipped only with the time-depth recorder during two years showing contrasting sea-ice and feeding conditions.

Penguins adapted their behaviour to both constraints by modulating the bottom phase of dives, i.e. the feeding phase, thus reflecting a change in prey availability. Extended bottom phases were related to longer recovery time, especially for deep dives. However it did not prevent penguins from exploiting the whole water column.

Finally, experimental and environmental constraints did not interact for any of the dive parameters, suggesting that penguins were able to adapt similarly to environmental constraints independently of their diving capacities.

Keywords: adaptability, foraging behaviour, penguins

INTRODUCTION

From a predator's perspective, environmental fluctuations may present a challenge since they may affect prey availability in terms of quantity, distribution and accessibility (Durant et al. 2007). Moreover, prey present characteristics such as the area where they live or their escape behaviour, which may force their predators to adjust their behaviour accordingly (Kato et al. 2001, Ropert-Coudert et al. 2002, Elliot et al. 2008, Miller & Trivelpiece 2008). Conversely, within a species, predators are assumed to present different intrinsic characteristics such as different capacities to catch prey (Ropert-Coudert et al. 2003, Woo et al. 2008). Because of their intrinsic foraging capacities, animals are expected to differ in their ability to adapt to extrinsic constraints such as environmental fluctuations. This may have implications in population dynamics if a certain category of the considered population is not able to adapt while others can (Sutherland 1996).

In seabirds, environmental fluctuations have been described to affect foraging trip duration, provisioning rate to offspring and ultimately reproductive success (e. g. Croxall et al. 1999, Kitaysky et al. 2000, Clarke et al. 2002, Pinaud & Weimerskirch 2002, Olmastroni et al. 2004, Emmerson & Southwell 2008, Nicol et al. 2008). Even though these fluctuations are likely to induce a modification of the foraging behaviour of animals, studies investigating at-sea behaviour in contrasting environmental conditions remain scarce (Kato et al. 2003, Lescroël & Bost 2005, Green et al. 2005). In addition, to our knowledge, no study on foraging behaviour simultaneously investigated extrinsic and intrinsic characteristics while both are expected to work concurrently.

To examine the influence of foraging constraints on foraging behaviour, Antarctic penguins represent a well-suited model. They live in a fluctuating environment characterized by sea-ice formation and sea-ice retreat. This sea-ice dynamics is strongly affected by climate changes (Stammerjohn et al. 2008) and, in some Antarctic regions, this has drastic repercussions on the whole ecosystem, including penguin populations (Moline et al. 2008). Therefore, it is crucial to understand ability of penguins to cope to their changing environment. One way to investigate this consists in examining penguin at-sea behaviour with data-loggers which have proved to be useful tools in research and conservation of seabirds (Ropert-Coudert & Wilson 2005, Burger & Shaffer 2008).

Here, we studied the diving behaviour of male Adélie penguins (*Pygoscelis adeliae*) under both environmental and experimental constraints. First we examined the diving behaviour of penguins in two consecutive summers showing contrasting environmental features that mimicked a general trend observed in some Antarctic regions, i. e. an early sea-ice retreat (Stammerjohn et al. 2008). Second, we mimicked a difference of intrinsic diving capacity between birds by equipping them with differently-sized, externally-attached instruments. In 2006-07, in Dumont d'Urville, Adélie Land, sea-ice retreated earlier than in 2007-08. As a result, penguins performed ~20% shorter foraging trips even after sea-ice had completely retreated in both years presumably because of different levels of food availability (Beaulieu et al. in press). In addition, in this study, external instrumentation was used to mimic different intrinsic diving capacities, since it has been associated to lower dive efficiency because of the induced additional drag in extremely hydrodynamic animals (Williams & Kooyman 1985, Lovvorn et al. 2001). To minimize the drag due to instrumentation, it is classically recommended attaching small (Culik & Wilson 1991) and streamlined instruments on the lower back of animals (Bannasch et al. 1994). It is assumed that instruments with a cross sectional area ≤ 1% of that of the animal do not induce an extra foraging cost (Culik & Wilson 1991). Here, to mimic two levels of diving capacity, we used two types of instrumentation representing ~1% and ~4% of the birds' cross sectional area, the latter size having been shown to lead to a ~70% increase in the foraging trip duration of Adélie penguins (Beaulieu et al. 2009). Both groups were monitored during the breeding seasons showing contrasting sea-ice conditions.

In this study, we investigated, at the dive scale, the consequences of both extrinsic and intrinsic-like constraints on the foraging behaviour of Adélie penguins in order to examine how penguins with variable diving capacities, are able to adapt to different environmental conditions.

MATERIAL AND METHODS

The study took place in the French polar station Dumont d'Urville (66°40'S, 140°01'E), Adélie Land, Antarctica, during the early chick-rearing period (guard stage) in austral summers 2006-07 and 2007-08 (further referred to as 2007 and 2008, respectively). In 2007, fast sea-ice retreated in late September while in 2008 it retreated, more typically three months later. In both years, the sea was free of ice during the guard stage.

Fieldwork

Because the foraging behaviour of male and female Adélie penguins differs (Clarke et al 1998), only males were included in this study. The experimental group was constituted by 14 male Adélie penguins among which seven (four equipped in 2007 and three equipped in 2008) were instrumented with an mk9 (Wildlife Computers, Redmond, WA, USA; 30g, 65x18x18mm) and seven (three equipped in 2007 and four equipped in 2008) had an mk9 and a dummy Plexiglas device (60g, 65x25x35mm). Penguins with mk9 only formed the control group and penguins with the dummy device and the mk9 constituted the handicapped group (hereafter reported as control and handicapped penguin respectively). Loggers and dummy devices were attached to feathers with mastic and Tesa® tape. Mk9 were attached in the midline of the lower back while dummy devices were attached ahead on the middle back. Penguins were equipped after egg hatching and both data loggers and dummy devices were recovered at the end of the guard stage.

Data analysis

All the loggers recorded depth every 5 seconds with 0.5 m resolution and an accuracy of ± 1%. After the recovery of devices, data were downloaded and analysed using IGOR software (Wavemetrics, version 5.0, USA). Only dives >1 m were included in the analysis. In total, 96973 dives were recorded. The start and end of the bottom phase of dives were defined as the first and the last time the rate of change of depth became <0.25 $m.s^{-1}$ during a dive (Ropert-Coudert et al. 2007a). The end of diving bouts was calculated according to the method of Gentry and Kooyman (1986) and only surface intervals within the bouts were included in the analyses on post-dive duration.

To compare the number of dives per foraging trip and the number of dives per hour between years and between control and handicapped birds, we used generalized linear models with the status (control *vs.* handicapped birds), the year and "status*year" as fixed factors.

Analyses of diving behaviour were conducted on the following dive parameters: maximum dive depth (m), dive duration (s), descent duration (s), descent rate ($m.s^{-1}$), bottom duration (s), number of undulations during the bottom phase (further referred to as number of wiggles and used as an index of feeding success; Bost et al. 2007), ascent duration (s), ascent rate ($m.s^{-1}$) and post-dive duration (s). To compare diving behaviour between the two groups, we used mixed models to avoid the problem of pseudoreplication since our statistical analyses involved repeated observations of the same subjects. Individuals were considered as random factors while the status, the year and "status*year" were used as fixed factors. Because the maximum depth during a dive influences all other dive parameters (Wilson et al. 1997, Cherel et al. 1999), we first added it as a covariate in the model to compare groups independently of depth. We then defined six depth classes (20, 40, 60, 80, 100 and 120 m) to assess the effect of the maximum depth on a given dive parameter. These depth classes were also used to compare the percentage of dives within each depth class between years and between control and handicapped penguins in a generalized linear model with the status, the year, the depth class and their interactions as fixed factors.

Analyses were conducted using SPSS 16.02 (SPSS Inc.) and JMP 8 (SAS Institute Inc.). Results are expressed as means ± SE and significance level was set at α=0.05.

RESULTS

Time spent underwater and number of dives

In a foraging trip, penguins performed similar number of dives whatever the year (2007: 819 ± 74 dives, 2008: 1005 ± 118 dives, Wald χ^2=1.91, df=1, P=0.17) or the status (control birds: 892 ± 64 dives, handicapped birds: 932 ± 127 dives, Wald χ^2=0.08, df=1, P=0.78) and the interaction "year*status" was not significant (Wald χ^2=0.30, df=1, P=0.58). However, they performed less dives per hour in 2007 than in 2008 (24.4 ± 1.4 and 29.6 ± 1.1 dives/hour, respectively, Wald χ^2=8.25, df=1, P=0.004). In contrast, the number of dives per hour was affected neither by the status (control birds: 28.8 ± 1.0 dives/hour, handicapped birds: 26.2 ± 1.4 dives/hour, Wald χ^2=0.76, df=1, P=0.38) nor by the interaction "year*status" (Wald χ^2=0.007, df=1, P=0.94).

Dive parameters

The distribution of dive depths depended neither on the year nor on the status ("year*depth class": Wald χ^2=4.70, df=5, P=0.45; "status*depth class": Wald χ^2=6.86, df=5, P=0.23; "year*status*depth class": Wald χ^2=6.60, df=5, P=0.25, Fig. 1).

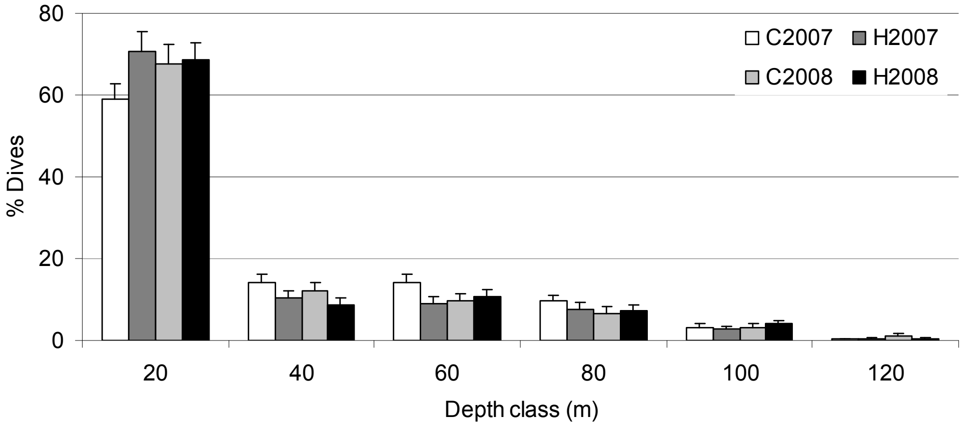

Fig. 1: Percentage of dives as a function of depth in control penguins in 2007 (C2007) and 2008 (C2008) and in penguins handicapped in 2007 (H2007) and 2008 (H2008). Data are presented as mean ± SE.

Maximum depth did not differ between years and statuses (Table 1). Independently of depth, the only dive parameters which changed both according to the year and the status were the number of wiggles and the bottom duration: penguins performed ~9% more wiggles during a ~12% longer bottom phase in 2007 than in 2008 and handicapped penguins performed ~9% more wiggles during an ~18% longer bottom phase than control birds (Table 1). Between two consecutive dives, penguins spent ~17% more time at the surface in 2007 than in 2008 (Table 1). This trend was also found in handicapped penguins that spent ~11% more time at the surface between two dives than control penguins, but this was not quite significant (Table 1). None of the other parameters differed between years or statuses and the interaction "year*status" was not significant for any of the dive parameters (all P>0.05).

Table 1: Dive parameters (mean ± SE) in 2007 and 2008 and in penguins equipped with a time-depth recorder (control) and in penguins equipped with a time-depth recorder and a handicap (handicap).

	2007	2008	F	P	Control	Handicap	F	P
Maximum depth (m)	25.83 ± 2.59	21.09 ± 2.62	1.88	0.20	24.28 ± 2.57	22.64 ± 2.64	0.23	0.64
Dive duration (s)*	69.07 ± 2.37	64.92 ± 2.37	1.59	0.24	65.12 ± 2.37	68.24 ± 2.40	0.91	0.36
Descent duration (s) *	20.62 ± 0.86	20.91 ± 0.86	0.06	0.81	20.97 ± 0.85	20.56 ± 0.86	0.12	0.74
Descent rate (m/s) *	0.77 ± 0.02	0.79 ± 0.02	0.45	0.52	0.79 ± 0.02	0.78 ± 0.02	0.02	0.90
Bottom duration (s) *	**24.58 ± 0.97**	**21.61 ± 1.01**	**6.85**	**0.02**	**20.73 ± 0.94**	**25.47 ± 1.04**	**17.31**	**0.002**
Number of wiggles *	**2.21 ± 0.05**	**2.02 ± 0.05**	**11.16**	**0.008**	**2.01 ± 0.05**	**2.22 ± 0.05**	**13.05**	**0.005**
Ascent duration (s) *	23.33 ± 1.11	21.97 ± 1.11	0.82	0.38	23.24 ± 1.10	22.06 ± 1.12	0.61	0.42
Ascent rate (s) *	0.70 ± 0.02	0.76 ± 0.02	2.79	0.13	0.72 ± 0.02	0.76 ± 0.02	0.06	0.80
Post dive duration (s)*	**30.14 ± 1.10**	**24.96 ± 1.13**	**11.42**	**0.01**	25.94 ± 1.10	29.15 ± 1.13	4.37	0.06

*Results with * were calculated with maximum depth as a covariate.*

Significant differences between groups are in bold.

Taking into account the depth class, the interactions "depth class*year" and "depth class*status" were all significant (all P<0.05) because of the strong influence of depth on any parameter (Fig. 2 & 3). Multiple comparisons revealed significant differences between years for bottom and post dive durations and for the number of wiggles (Fig. 2). Bottom duration and wiggles were increased in 2007 compared to 2008, when penguins reached at least a 60 m depth. In contrast, post dive durations were longer in 2007 than in 2008 for deeper dives (≥ 80 m). The same influence of depth was found in handicapped penguins for whom dive, descent, bottom and post dive durations were longer than in control birds for very deep dives only (≥ 100 m, Fig. 3) while bottom duration was significantly longer in handicapped penguins for shallower dives (40-60 m).

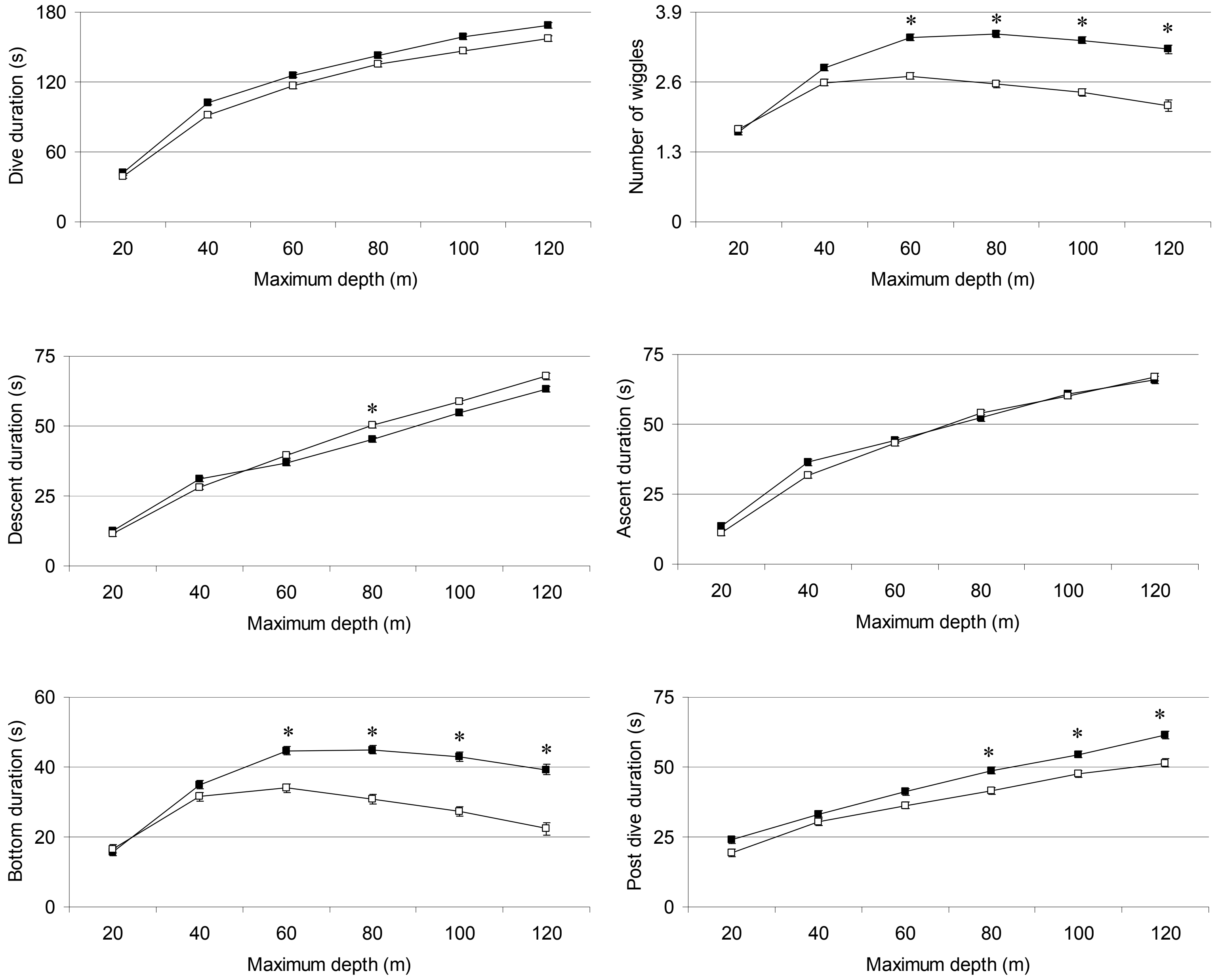

Fig. 2: Dive parameters as a function of depth in 2007 (black symbols) and 2008 (white symbols). Data are presented as mean ± SE.

** indicates a significant difference between the two years for a given depth class.*

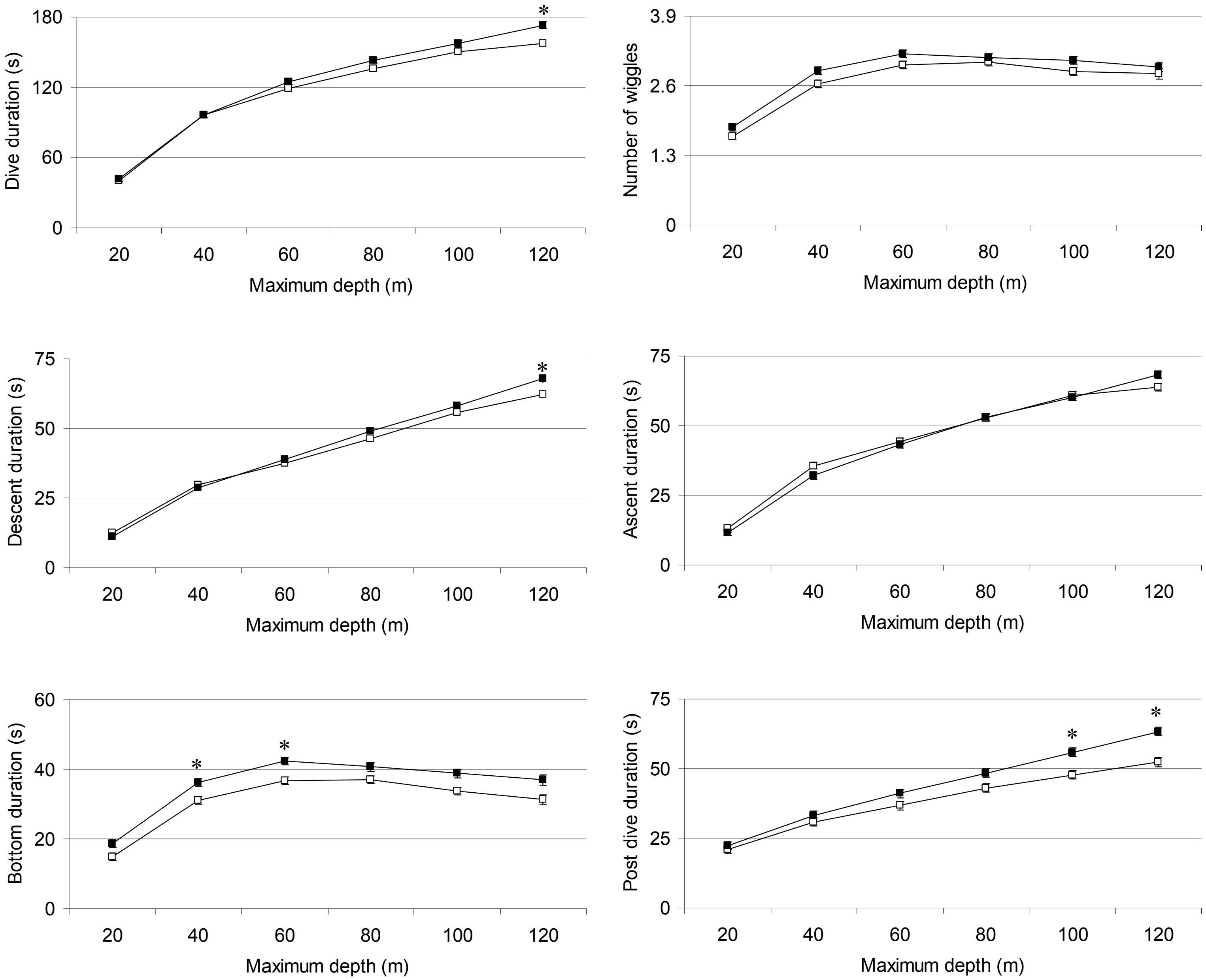

*Fig. 3: Dive parameters as a function of depth in penguins instrumented with a time-depth recorder (white symbols) and in penguins equipped with a time-depth recorder and a handicap (black symbols). Data are presented as mean ± SE. * indicates a significant difference between the two statuses for a given depth class.*

DISCUSSION

Our study highlights the plasticity of the foraging behaviour of Adélie penguins when they face extrinsic or intrinsic-like diving constraints. In response to a diving constraint and whatever its nature, Adélie penguins adjusted specific components of dives especially the bottom duration and the number of wiggles. As a consequence, the bottom phase can be considered as the main dive component that allows penguins to adapt to changing foraging conditions. This conclusion is confirmed by other studies examining the diving behaviour of penguins that also found that the birds modulated the bottom phase in response to different constraints (Green et al 2005, Lescroël & Bost 2005, Ropert-Coudert et al. 2007a, b).

In Adélie penguins, ~70% of prey items are captured during the bottom phase (Ropert-Coudert et al. 2001) so that the modulation of this dive component is likely to reflect a change in prey availability or quality. Indeed, Green et al. (2005) reported that macaroni penguins *Eudyptes chrysolophus* spent more time at the bottom in winter than in the breeding season, presumably because of lower food availability in winter. Similarly, Lescroël & Bost (2005) showed that the bottom duration was extended when gentoo penguins *Pygoscelis papua* fed more predominantly on fish than on krill.

The timing of sea-ice retreat has been described to affect primary production in the water column and the density of krill *Euphausia superba* (Quetin & Ross 2001), the main prey of Adélie penguins in several Antarctic localities (Ridoux & Offredo 1989, Clarke et al. 1998, Wienecke et al. 2000, Ropert-Coudert et al. 2002). In 2006-07, in Dumont d'Urville, sea-ice retreated earlier than in 2007-08, and penguins performed ~20% shorter foraging trips and penguins' diet was characterised by a slightly higher contribution of fish (Beaulieu et al. in press). This suggests that environmental conditions between the two years may have affected krill availability and that fish was used as an alternative prey to krill. This change in the penguins' diet may have forced the birds to spend more time at the bottom and perform more wiggles, which resulted in a higher effort as suggested by longer recovery durations at the surface. However in 2007, the number of dives per hour of foraging trip was lower than in 2008 thus balancing this extra diving cost. Similarly to our study, it has been found that Adélie penguins feeding on krill or on fish reached the same maximum depth in Dumont D'Urville (Ropert-Coudert et al. 2002) and Syowa (Kato et al. 2003). This contrasts with the situation in Adélie penguins in other locations (Endo et al. 2000) and in the closely-related chinstrap *Pygoscelis antarctica* (Miller & Trivelpiece 2008) and gentoo penguins (Croxall et al. 1988) who dove deeper when feeding more predominantly on fish. As the dive maximum depth reflects the depth distribution of prey, this suggests that prey upon which Adélie penguins feed (krill or fish) near Dumont d'Urville are distributed similarly in the water column but this situation may change according to locations.

In contrast to environmental conditions, the contribution of krill to the penguins' diet was similar between control and handicapped penguins (Beaulieu et al. unpublished data) so that the lengthening of the bottom phase and the associated higher number of wiggles do not reflect a change of diet in handicapped penguins but presumably the difficulty of catching prey efficiently (in that case, a wiggle would reflect both successful and unsuccessful attempts to catch prey) and/or the need to energetically compensate for the extra cost due to the handicap.

In handicapped penguins, the 40-60 m depth class seems more profitable since, in this range, penguins could extend bottom duration and thus the probability of encountering prey, without incurring an additional cost, as reflected by the absence of significant increase in the recovery time at the surface (Fig. 3). Nevertheless, handicapped penguins did not preferentially exploit this depth class. Instead, they used the whole water column like controls, and performed very deep dives (Fig. 1) even though those dives induced an extra cost (Fig. 3). This extra cost incurred by deep dives was also more important in 2007 than in 2008 (Fig. 2), but similarly to handicapped penguins, penguins in 2007 did not avoid deep depth classes (Fig. 1). This indicates that the additional cost associated with deep dives is not sufficient to prevent penguins from performing these expensive dives. This may be due to vertical movements of prey with for instance, krill distribution being deeper during the day than during the night (Gaten et al. 2008).

Interestingly, the two constraints that we considered in the present study did not interact for any of the dive parameters: neither the handicap heightened the influence of the year nor the year heightened the effect of the handicap on dive parameters. Whatever the dive capacity of penguins, they were all able to adapt similarly to fluctuating environmental constraints. This suggests that, within a population, all the categories of birds in terms of diving capacity, would be equally affected by altered environmental conditions. However our study focused only on breeding males with two levels of diving capacity and it included only two environmental conditions. In reality, a population does not work on a binary mode with efficient and deficient foragers but includes individuals showing variable characteristics (e. g. sex, age, breeding status); the spectrum of diving capacities within a population of Adélie penguins and that of environmental conditions in Antarctica are therefore much broader than considered in the present study. Despite this limitation, our study is a preliminary approach to understand how environmental constraints affect individuals with different foraging capacities. In this line of thought, it would be worthwhile conducting further studies considering together more intrinsic and extrinsic conditions to examine more precisely how penguins with variable diving capacities can or cannot adapt to changing environmental conditions in Antarctica.

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Article 5 : Réponse écophysiologique à la contrainte expérimentale

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ECOPHYSIOLOGICAL RESPONSE OF ADÉLIE PENGUINS FACING AN EXPERIMENTAL INCREASE IN BREEDING CONSTRAINTS

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Ecophysiological response of Adélie penguins facing an experimental increase in breeding constraints

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SUMMARY

Foraging strategies play a key role in breeding effort. Little is known, however, about their connection with hormonal and nutritional states, especially when breeding constraints vary. Here, we experimentally increased foraging costs and thus breeding constraints by handicapping Adélie penguins (*Pygoscelis adeliae*) with dummy devices representing 3–4% of the penguins' cross-sectional area. We examined food-related stress (*via* plasma corticosterone concentration) and nutritional state (*via* metabolite levels). Concurrently, we investigated the use of ecological niches *via* the isotopic signature of red blood cells indicating the trophic position (δ^{15}N) and the spatial distribution (δ^{13}C) of penguins. Handicapped birds performed ~70% longer foraging trips and lost ~60% more body mass than controls and their partners. However, corticosterone levels and the nutritional state were unchanged. The isotopic signature revealed that males and females differed in their foraging behaviour: upper trophic levels contributed more in the males' diet, who foraged in more pelagic areas. Handicapped and partner birds adopted the same strategy at sea: a shift towards higher δ^{13}C values suggested that they foraged in more coastal areas than controls. This change in foraging decisions may optimize feeding time by decreasing travelling time. This may partly compensate for the presumed lower foraging efficiency of handicapped birds and for the energetic debt of their partners who had to fast ~70% longer on the nest. We propose that this flexible use of ecological niches may allow birds facing increased breeding constraints to avoid a chronic stress and to minimize the impact on their body condition.

Key words: corticosterone, foraging, handicap, isotopic signature, metabolite, stress.

INTRODUCTION

In an unpredictable environment, breeding constraints may vary between years or within one single reproductive season. To cope with these fluctuating breeding constraints, animals have to be able to adapt and change their behaviour accordingly. One major component of reproductive effort is foraging activity. Several studies have examined whether animals are able to modify their foraging behaviour according to different breeding constraints, in different foraging locations (Wienecke et al., 2000; Tremblay and Cherel, 2003; Lescroël and Bost, 2005), under different environmental conditions (Green et al., 2005; Yoda and Ropert-Coudert, 2007) or at different stages of the breeding cycle (Clarke et al., 1998; Clarke, 2001).

Though changes in foraging behaviour provide worthwhile information on the response of parents when facing variable breeding constraints, understanding of the regulation of animal behaviour can be further enhanced by the examination of a combination of physiological parameters. These may provide useful information on: (1) food-related stress, (2) nutritional condition and (3) the use of ecological niches by experimental animals (Kern et al., 2007; Navarro and González-Solís, 2007; Navarro et al., 2008).

Glucocorticoids play an important role in the regulation of feeding, locomotor activity and energy metabolism (see Landys et al., 2006). For instance, in Adélie penguins (*Pygoscelis adeliae*, Hombron and Jacquinot 1841), baseline corticosterone levels have been correlated with foraging behaviour (Angelier et al., 2008). Moreover, corticosterone is a stress hormone that increases when parents have to work harder (Storey et al., 2006) or when they have to face an unpredictable situation (Pravosudov et al., 2001; Reneerkens et al., 2002). Finally, corticosterone levels have been proposed as a reliable measure of food-related stress and, as a consequence, a direct measure of food availability in free-living birds (Kitaysky et al., 2007).

Changes in foraging decisions may also affect the nutritional state of parents. For this purpose, metabolites can be used as indicators of the nutritional state in free-living animals (Jenni-Eiermann and Jenni, 1998). For example, plasma triglyceride concentration is an indicator of fattening because it increases with the amount of food absorbed and it decreases during heavy endurance exercise. An increase in uric acid levels characterizes the rise in protein breakdown which occurs once a critical threshold has been reached in the depletion of body fuel reserves (see Lindström and Piersma, 1993) or may result from higher muscle activity and from a higher dietary protein fraction. It is also useful to investigate metabolites and hormone levels in parallel as glucocorticoids may increase protein breakdown (Jenni et al., 2000) and decrease plasma triglyceride levels (Remage-Healey and Romero, 2001; Kern et al., 2007).

The measurement of stable isotope ratios is a valuable tool for examining the use of ecological niches by animals (Kelly, 2000; Inger and Bearhop, 2008). The concept of the isotopic method is that animals are constituted by what they consume. For example, as trophic level increases, the quantity of ^{15}N increases, so the ratio ^{15}N/^{14}N (expressed as δ^{15}N) indicates the trophic position of the consumer (Bearhop et al., 2002). The ratio $^{13}C/^{12}C$ (expressed as $\delta^{13}C$) is more stable in marine foodwebs and its variation instead reflects the spatial distribution of consumers (Inger and Bearhop, 2008), with high values being found in coastal foragers and low values in pelagic foragers (Hobson et al., 1994; Cherel and Hobson, 2007). The isotopic signature of the consumer thus reflects the isotopic signature of the consumed prey species.

The main goal in the present study was to enhance the understanding of foraging decisions in Adélie penguins when they face an increase in their breeding constraints. We increased the foraging cost of breeding males and females by equipping them with large dummy devices known to affect the drag of these streamlined animals (Culik and Wilson, 1991; Culik and Wilson, 1992; Watanuki et al., 1992; Miller and Davis, 1993). We thus examined the consequences of this experimental increase in foraging cost on foraging trip duration, body mass loss and the profile of physiological parameters. Handicapped birds were expected to be exposed to a chronic stress due to the presence of the instrument and the difficulty it causes in catching prey efficiently, as well as to an extra foraging cost. In addition, if handicapped birds performed longer foraging trips, their partners were expected to endure longer fasting periods on the nest and consequently to face an additional energetic debt when returning to the sea to feed. For these reasons, we expected corticosterone levels to increase in handicapped and partner birds. Moreover, we expected a decrease in triglyceride levels and an increase in uric acid concentrations in handicapped birds because they would have to make a greater effort (Culik and Wilson, 1991) while being less efficient at catching prey (Ropert-Coudert et al., 2007).

MATERIALS AND METHODS

Study species and area

Fieldwork was carried out during the austral summer 2006–2007 in Dumont d'Urville (66°40′S; 140°00′E), Adélie Land, Antarctica. The Adélie penguin breeding cycle comprises four phases: courtship, incubation [males are in charge of the first incubation shift (~12 days) while females re-feed at sea], guard stage (when the two parents alternate foraging at sea and chick attendance at the nest) and crèche stage (when the two parents forage at the same time leaving the young alone on the colony). This study focused on the incubation and the guard stage, because during the crèche stage it was impossible to precisely monitor the birds.

Thanks to the method of stomach flushing (Ridoux and Offredo, 1989; Kent et al., 1998; Wienecke et al., 2000; Ropert-Coudert et al., 2002; Libertelli et al., 2003), Adélie penguins are known to prey upon two trophic levels: krill (mainly *Euphausia superba* and *Euphausia cristallorophias*) and fish (mainly *Pleuragramma antarcticum*). These prey species have been segregated by their overall isotopic signature in Adélie Land, Antarctica: *Euphausia superba* constitutes a lower trophic level than fish and lives in more oceanic areas (Cherel, 2008). In addition, diet determined by stable-isotope analysis closely mirrors that determined from stomach content (Tierney et al., 2008) and there is a positive relationship between the proportion of fish consumed by Adélie penguins and their $\delta^{15}N$ values (Ainley et al., 2003).

Study protocol

This study was approved by the ethics committee of the French Polar Institute Paul Emile Victor.

Eighty individuals belonging to 40 pairs were followed. A few days before egg laying, the birds were weighed (electronic balance, ±2 g; Ohaus, source?) and individually marked for identification with a subcutaneous transponder and a letter painted on their chest with Nyanzol-D, and some of them were handicapped (see below). Sex was determined *a posteriori* by using a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor, 1962; Kerry et al., 1993).

From the beginning of the incubation period to the crèche stage, we increased the cost of foraging by equipping one bird per pair (*N*=25 birds) with a large dummy Plexiglas device (25 mm×35 mm×60 mm, 60 g) attached with mastic, cyanoacrylate glue, Tesa tape and cable ties to the middle back feathers (Wilson et al., 1997). When considering the deleterious effects of instrumentation in diving animals, three main parameters have to be taken into account (Bannasch et al., 1994): (1) the shape of the device, (2) the attachment position and (3) the cross-sectional area (CSA) of the device relative to the animal's CSA. The consensus recommends attaching hydrodynamic instruments on the lower back, with a CSA of less than 1% of that of the animals, so as to prevent the generation of extra drag and extra foraging cost (Culik and Wilson, 1991; Bannasch et al., 1994). In the present study, the dummy devices were parallelepipeds (not hydrodynamic), attached to the middle back and their CSA represented 3–4% of the penguins' CSA. An instrument with a CSA 3.5% that of the penguin is likely to produce a drag similar to that of the bird (Bannasch et al., 1994). In addition, Culik and Wilson (Culik and Wilson, 1991) reported that the cost of transport was increased by 25% in penguins equipped with instruments representing ~2% of their CSA. As a result, we can confidently assume that our dummy devices increased the foraging cost of handicapped penguins. However, the size of the dummy device was chosen so as not to be too deleterious for the birds, according to previous studies which used devices of comparable size on Adélie penguins (Culik and Wilson, 1991; Culik and Wilson, 1992; Watanuki et al., 1992; Miller and Davis, 1993).

In total, 15 pairs were assigned to the control group (where neither mate in a pair was handicapped), 12 pairs to the handicapped-female group (where only the females were equipped with the device) and 13 pairs to the handicapped-male group (where only the males were equipped with the device). We distinguished three treatments at the pair level (control, handicapped-female and handicapped-male pairs), therefore resulting in six treatments at the parent level (Table 1).

Foraging trip duration was determined by visual nest observation ranging from every 2 h to continuous. The birds were captured and weighed a second time during the guard stage (40–45 days after egg laying), after a nest relief and just before leaving the colony to forage at sea. Body mass loss was defined as the difference between the first and the second weighing. Blood was collected from the wing vein with a heparinized syringe and centrifuged. Plasma and red blood cells were then quickly stored at –20°C. Because the capture and restraint constitute an acute stress which may influence baseline blood parameters (Jenni-Eiermann and Jenni, 1998; Cockrem et al., 2008), great attention was paid to minimizing the stress for the birds. The pengiun's head was covered by a hood (Cockrem et al., 2008) and handling duration was minimized and measured from the approach of the experimenter towards the nest until the end of blood sampling. A 5 min threshold was chosen as it has been shown that handling durations of less than 5 min had no effect on corticosterone levels in Adélie penguins (Vleck et al., 2000). Blood sampling depended on the bird departure and therefore occurred at any time of the day. Note that in Adélie penguins, no daily rhythm of corticosterone secretion has been reported (Vleck and Van Hook, 2002; Angelier et al., 2008).

Table 1. Foraging trip duration, body mass loss and physiological parameters of Adélie penguins according to their sex and their status (control, handicapped or partner birds)

	Control pairs (*N*=15)		Handicapped-female pairs (*N*=12)		Handicapped-male pairs (*N*=13)	
	Control males	Control females	Partner males	Handicapped females	Handicapped males	Partner females
Foraging trip duration (days)	0.97±0.28	1.02±0.28	1.01±0.31	1.84±0.72	1.62±1.08	1.05±0.29
Body mass loss (g)	504±288	386±260	487±320	696±198	752±274	378±234
[Corticosterone] (ng ml^{-1})	2.49±2.55	1.56±1.34	3.35±2.57	2.14±1.64	2.92±3.24	1.59±1.56
[Triglycerides] (mmol l^{-1})[a]	1.21±0.53	1.14±0.51	1.50±0.71	1.28±0.43	1.60±0.50	1.41±0.49
[Uric acid] (mmol l^{-1})	0.30±0.11	0.34±0.16	0.29±0.15	0.36±0.18	0.31±0.16	0.35±0.16

Data are means ± s.d.

Partner birds formed pairs with handicapped birds.

[a] [Triglycerides] corresponds to estimated marginal means obtained by a general linear model with handling time as a covariate.

Laboratory analyses

Analyses of the plasma concentrations of corticosterone, triglycerides and uric acid were carried out at the IPHC-DEPE, France. Corticosterone levels were determined by immunoassay (Assay Pro, AssayMax Corticosterone ELISA Kit, Town, State, Country) and concentrations of triglycerides and uric acid were measured using enzymatic colorimetric tests (Sigma Diagnostic, St Louis, MO, USA). Intra-assay and inter-assay coefficients of variation were between 1% and 3% for metabolite measurements and were 5% and 7%, respectively, for corticosterone measurements.

Tissue isotopic signature mirrors the diet throughout the period of tissue synthesis (Bearhop et al., 2002). For the birds of this study, the period between the first time they fed at sea and blood sampling was 37.6±2.0 days for females and 25.1±3.2 days for males (means±s.d.). This time corresponds to the turnover of red blood cells (Hobson and Clark, 1993; Haramis et al., 2001; Bearhop et al., 2002). For these reasons, we chose to investigate isotopic signature in red blood cells because it reflects the diet of birds over the whole study period. Before isotopic analyses, red blood cells were lyophilized (48 h) and powdered (Hobson et al., 1997) but were not delipidated (Cherel et al., 2005). Stable carbon and nitrogen isotope assays were carried out at the Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA), L'Houmeau, France. Intra-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0.88% and 0.63%, respectively. Inter-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0.42% and 0.24%, respectively. Results are expressed in the standard δ notation (‰) relative to PDB (Peedee belemnite) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

Data analyses

Body mass and body mass changes were compared between groups with general linear models. Comparisons of foraging trip duration were performed using a generalized linear model with a gamma distribution. For these comparisons, we considered only the guard stage period because corticosterone levels and nutritional state measured 40–45 days after egg-laying should better reflect this period.

For plasma parameters, we first checked whether handling duration was correlated with the plasma concentrations of corticosterone, triglycerides and uric acid, using Spearman correlations. Then, to compare these plasma concentrations between the different groups of birds, we used general linear models. If handling duration was correlated with the considered parameter, it was added as a covariate in the model. Normality of residuals was assessed using a Shapiro–Wilk test. When this condition was not fulfilled (corticosterone), we used a generalized linear model with a gamma distribution.

Analyses were conducted using SPSS 16.02 (SPSS, Chicago, IL, USA). Results are expressed as means ± s.d. and significance level was set at α=0.05.

RESULTS

Foraging trip duration

During the guard stage, bird treatment affected foraging trip duration (Wald χ^2=70.33, d.f.=2, P<0.001) with handicapped birds performing longer foraging trips (1.73±0.91 days) than control birds (1.00±0.28 days, P<0.001) and partner birds (1.03±0.30 days, P<0.001). In contrast, foraging trip duration was not influenced by the sex of the bird (Wald χ^2=2.78, d.f.=1, P=0.10) or by the interaction between the sex and the treatment of the bird (Wald χ^2=0.99, d.f.=2, P=0.61, Table 1).

Body mass

Bird body mass was similar during the courtship period between the three treatment groups ($F_{2,66}$=0.42, P=0.66) and between the treatment groups within males and females (interaction sex×treatment, $F_{2,66}$=1.21, P=0.31). However, during the courtship period, males were heavier than females (5.17±0.45 and 4.60±0.27 kg, respectively; $F_{1,66}$=39.13, P<0.001).

Forty to forty-five days after egg laying, handicapped birds had lost ~60% more mass (724±233 g, $F_{2,64}$=8.25, P=0.001) than control birds (445±276 g, P=0.002) and partner birds (432±285 g, P=0.003). Male and female birds lost body mass at the same rate ($F_{1,64}$=2.10, P=0.15) and the interaction sex×treatment was not significant ($F_{2,64}$=0.09, P=0.92, Table 1).

Effects of handling duration

Corticosterone levels and plasma concentrations of uric acid were not correlated with handling duration (Spearman correlations: R=–0.13, P=0.26; R=–0.05, P=0.63, respectively). However, plasma concentrations of triglycerides were correlated with handling duration (Spearman correlation, R=–0.42, P<0.001).

Corticosterone

Corticosterone levels were higher in males than in females (2.92±2.81 and 1.77±1.50 ng ml^{-1}, respectively; Wald χ^2=4.71, d.f.=1, P=0.03) but were not affected by the treatment or the interaction sex×treatment (Wald χ^2=0.86, d.f.=2, P=0.65 and Wald χ^2=0.57, d.f.=2, P=0.75, respectively; Table 1).

Triglycerides

Males and females exhibited similar plasma concentrations of triglycerides (1.43±0.62 and 1.27±0.49 mmol l^{-1}, $F_{1,69}$=1.83, P=0.18). This concentration did not significantly differ between the different treatment groups ($F_{2,69}$=2.52, P=0.09). In addition, the interaction sex×treatment was not significant ($F_{2,69}$=0.45, P=0.64; Table 1).

Uric acid

Plasma concentrations of uric acid did not differ between males and females (0.30±0.14 and 0.35±0.16 mmol l^{-1}; respectively, $F_{1,79}$=2.37, P=0.13) and between the different treatment groups ($F_{2,79}$=0.01, P=0.91). The interaction sex×treatment was also not significant ($F_{2,79}$=0.05, P=0.95; Table 1).

Isotopic signature

Males had higher values of δ^{15}N (8.93±0.34‰, $F_{1,71}$=11.03, P=0.001) and lower values of δ^{13}C (–24.60±0.24‰, $F_{1,71}$=17.07, P<0.001) than females (δ^{15}N=8.67±0.36‰, δ^{13}C=–24.31±0.38‰). The value of δ^{15}N was not significantly affected by the treatment ($F_{2,71}$=2.36, P=0.10) whereas the value of δ^{13}C differed according to the treatment ($F_{2,71}$=5.22, P=0.008), with control birds presenting lower values than partner birds (P=0.02) and handicapped birds (P=0.01). In contrast, handicapped and partner birds presented similar δ^{13}C values (P=0.84). The interaction sex×treatment was not significant for δ^{15}N ($F_{2,71}$=1.67, P=0.20) or for δ^{13}C ($F_{2,71}$=0.44, P=0.65; Fig. 1).

DISCUSSION

Sex-specific foraging strategies

Our results highlight variable ecophysiological trends according to the sex or the treatment of birds. First, we confirmed the sex-specific foraging behaviour of Adélie penguins (Clarke et al., 1998). Males had higher values of δ^{15}N and lower values of δ^{13}C than females, suggesting that higher trophic levels contributed more to the diet of males than to that of females and that males tended to forage in more pelagic areas than females. Using the model proposed by Tierney and colleagues (Tierney et al., 2008) and the isotopic signature of prey (*E. superba* and *P. antarcticum*) given by Cherel (Cherel, 2008), krill contribution for females' diet was 42% while it was 37% for males' diet. The difference in δ^{15}N values between males and females was small but Ainley and colleagues (Ainley et al., 2003) found a positive relationship between the proportion of fish consumed by Adélie penguins and δ^{15}N values over a relatively small range of δ^{15}N values. δ^{15}N measurement therefore appears to be a sensitive tool able to detect small differences in the diet of animals. Moreover, our results on trophic levels *via* δ^{15}N values confirmed what is known about the diet of Adélie penguins: males and females both feed on krill (lower trophic level) but males feed more extensively on fish (higher trophic level) than females (Clarke et al., 1998; Tierney et al., 2009). This trophic difference between males and females is not exceptional in animals, particularly amongst penguins (Volkman et al., 1980; Forero et al., 2002; Forero et al., 2005; Norris et al., 2005; Bearhop et al., 2006; Awkerman et al., 2007). This may be due to different feeding requirements and/or foraging capacities between males and females and may serve to reduce the intra-specific competition on feeding grounds. Moreover this difference in the use of the habitat between males and females may be modulated by corticosterone levels, which are known to affect feeding behaviour and locomotor activity. The 60% higher corticosterone levels in males may drive them to forage in more pelagic areas. To confirm this hypothesis, further studies should experimentally modulate corticosterone levels and examine simultaneously the consequences in terms of the use of the habitat by males and females.

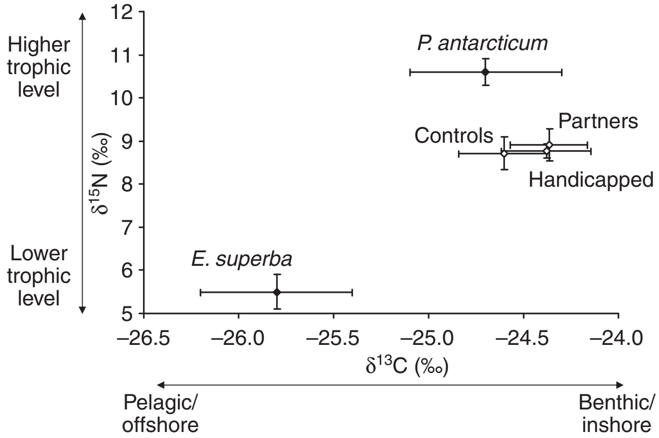

Fig. 1. δ^{15}N and δ^{13}C values of Adélie penguins (open symbols) and their prey (filled symbols). Values for prey come from Cherel (Cherel, 2008). Results are presented as means ± s.d.

Foraging strategies of handicapped penguins and their partners

As shown by prolonged foraging trips in handicapped birds, the handicap affected foraging behaviour. Consequently, we first hypothesized that handicapped and partner birds were exposed to a situation of stress (longer foraging trips for handicapped birds, suggesting a lower foraging efficiency, and prolonged fasting periods for their partners) so corticosterone levels should have increased and nutritional state should have been altered. However, our results show that handicapped and partner birds maintained their corticosterone levels and their nutritional state in a range comparable to that of control birds. Even in handicapped birds, in which body mass loss was increased (Table 1), corticosterone levels and nutritional state remained unchanged. In our study, corticosterone levels were low but comparable to those measured in Adélie penguins by Cockrem and colleagues (Cockrem et al., 2008), just after bird capture, so we can be confident that these values reflect baseline corticosterone levels. This consistency in corticosterone levels was also found in handicapped pied flycatchers *Ficedula hypoleuca* (Kern et al., 2007) and Cory's shearwaters *Calonectris diomedea* (Navarro et al., 2008).

At the beginning of the experiment, the handicap may have elevated corticosterone levels but this increase may have been only temporary (Suedkamp Wells et al., 2003). Several non-exclusive hypotheses may explain why corticosterone levels were not increased several weeks after the beginning of the experiment: (1) the handicap did not represent a significant chronic stress, (2) birds may have habituated to the stressor, (3) birds may have changed their foraging decisions to avoid a chronic stress. Indeed, as the stressor was always the same throughout the experiment, after some time its effects would no longer be unpredictable and thus the handicap probably would not represent a stressor anymore (hypothesis 1). Moreover, animals are expected to avoid situations of chronic stress to remain healthy because chronic stress is associated with physiologically deleterious effects (Sapolsky et al., 2000). To this end, after a repeated or a chronic exposure to a stressor, an animal is expected to habituate (Fig. 2) and to reduce its glucocorticoid response through an acceptation of the stressor and/or physiological feedback (hypothesis 2) (Romero, 2004).

In our study, birds even seem to have coped with the stressor, as they changed their foraging strategies (hypothesis 3, Fig. 2): they still fed on the same trophic levels but foraged in more coastal areas as suggested by the small but significant shift towards higher δ^{13}C

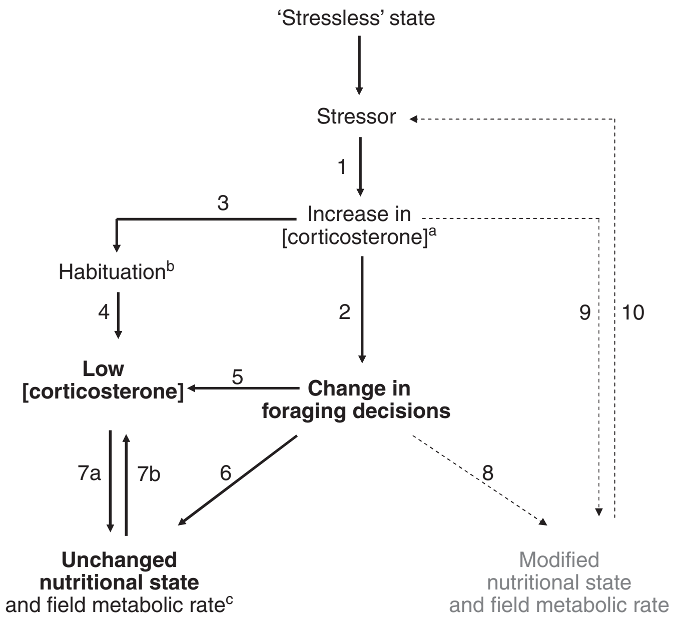

Fig. 2. Schematic view showing the potential ecophysiological responses of Adélie penguins to increased breeding constraints. Superscript letters refer to data from other studies, potentially transposable to our study (^{a}Suedkamp Wells et al., 2003; ^{b}Romero, 2004; ^{c}Culik and Wilson, 1992). Data in bold were obtained in this study and bold arrows indicate the most probable linkage between these data. In our study, the stressors we considered were the low foraging efficiency due to the large dummy device attached to handicapped penguins and the prolonged periods of fasting for their mates. This may have led to a temporary increase in corticosterone levels (arrow 1) but the birds may have solved this stressful situation by foraging in more costal areas thus optimizing feeding time at the expense of travelling time (arrow 2). This behavioural change, associated with habituation to the stressor, for instance through an acceptation of the stressor and/or physiological feedback (arrow 3), may explain the low corticosterone levels (arrows 4 and 5) and unchanged nutritional state and field metabolic rate (arrows 6 and 7a). Conversely, unchanged nutritional state and metabolic rate may also allow corticosterone levels to remain low (arrow 7b). Though not observed in our study, other responses could have occurred: changes in foraging behaviour could have been insufficient to cope with the stressor (arrow 8) or could have not occurred at all (arrow 9), thus resulting in modified nutritional state and field metabolic rate. Finally, the modified nutritional state and field metabolic rate could be perceived as a potential stressor (arrow 10), thus resulting in a vicious circle, which does not seem viable over a long time scale.

values in handicapped penguins. Interestingly, Navarro and Gonzáles-Solís (Navarro and Gonzáles-Solís, 2007) found that handicapped Cory's shearwaters also modified their spatial distribution in the Atlantic Ocean (although δ^{13}C values remain constant) but did not change their diet (as suggested by constant δ^{15}N values). In our study, the difference in δ^{13}C values might be due to a difference in metabolic rate between handicapped and control penguins, but Carleton and Martínez del Rio (Carleton and Martínez del Rio, 2005) found in birds that an increased metabolism had no effect on the rate of ^{15}N incorporation into red blood cells and had a very small effect on the rate of ^{13}C incorporation. In addition, in our study, partner and control birds that were supposed to present similar metabolic rates, nevertheless exhibited different isotopic signatures. This suggests that the different δ^{13}C values observed between the experimental groups cannot be (fully) explained by different isotopic incorporation rates. In our study, the difference in δ^{13}C values between groups was small presumably because our δ^{13}C values encompassed several consecutive foraging trips, which were not necessarily all coastal. Yet, the resulting average still indicates that the overall δ^{13}C values were significantly smaller in controls than in other groups. The strategy of foraging in more coastal waters may allow birds to optimize feeding time by reducing travelling phases (back and forth) between the colony and the feeding grounds. The presumably lower efficiency of handicapped birds while travelling, diving and catching prey is likely to explain this change in their foraging behaviour. Culik and Wilson (Culik and Wilson, 1991) reported that instrumented Adélie penguins, swimming in a canal, had a 25% higher swimming metabolic rate than controls but they paradoxically found that the field metabolic rate during one foraging trip at sea was similar to that of controls (Culik and Wilson, 1992). They suggested that this discrepancy was possible if the foraging range was reduced. Our present data may confirm this hypothesis as instrumented penguins foraged in more coastal areas, presumably less distant than offshore areas.

Surprisingly, the partners of handicapped penguins adopted the same strategy as their mates. Because of the prolonged trips of handicapped birds, partners had to fast ~70% longer at the nest than control birds and therefore had an energetic debt when returning at sea to feed. If we consider that penguins lose 50 g per day when fasting (Chappell et al., 1993), the partners of handicapped penguins should have weighed approximately 250 g less than controls when they were weighed during the guard stage. Moreover, considering that the energy cost of fat and protein deposition is $53\,\mathrm{kJ\,g^{-1}}$ and that krill has a metabolizable energy content of $3.5\,\mathrm{kJ\,g^{-1}}$ (Chappell et al., 1993), partner birds would need an additional 3.8 kg of krill to compensate for their prolonged fasting periods. To maintain their body mass constant (Table 1), the alternatives for them could be: (1) to lengthen the duration of their foraging trips to catch more prey items, (2) to reduce the quantity of food given to the chicks or (3) to increase the rate of prey capture per foraging trip. The first strategy was not observed in our study while the other two seem possible. In addition, the data from our study give some support to the third hypothesis: the δ^{13}C signature showed that partner birds foraged in more coastal waters than control birds thus probably reducing travelling phases and optimizing feeding time per foraging trip. It would be worthwhile examining whether the same foraging strategy is adopted by penguins in natural conditions (i.e. poor food conditions) obliging the penguins to forage for longer and then forcing their partners to fast longer on the nest.

However these results raise a new question: why did control penguins not optimize their foraging trips similarly? One reason may be that they avoided a higher feeding competition in coastal areas by foraging offshore. Another hypothesis explaining the difference between control and handicapped penguins is that coastal waters are more predictable (Weimerskirch, 2007) but less productive than oceanic areas. Handicapped penguins were unable to forage and/or could not 'take the risk' of foraging in unpredictable oceanic waters even though these may be more productive. Partners of handicapped birds adopted a similar cautionary strategy and chose to forage in coastal waters in response to the long trips of their handicapped mates. In contrast, control birds with better foraging ability may be more flexible in exploring their environment and thus may be better able to cope with resource unpredictability and may find oceanic waters to be more productive grounds.

In our study, handicapped penguins opted for changing their foraging behaviour and not abandoning their breeding attempt, while sacrificing their body condition. This suggests that Adélie penguins can tolerate a lower body condition when breeding constraints increase. However, such a strategy is not expected in long-lived animals that should prioritize their body maintenance. This may be because the body condition of handicapped penguins was not drastically altered. Indeed, Adélie penguins are able to support severe body mass losses (more important than that experienced by handicapped individuals) during their breeding cycle and particularly when they incubate (Cockrem et al., 2006). Even though handicapped individuals lost more body mass than control birds, this mass loss was in the physiological range for this species. In addition, abandoning their breeding attempt would obviously have allowed handicapped penguins to forage only for themselves but it would also have implied negative effects: (1) no breeding success the year they were handicapped and (2) a potentially diminished breeding success the subsequent year. Indeed, information on breeding performance can affect the probability of divorce (Dubois and Cézilly, 2002), potentially altering breeding success in Adélie penguins (Ainley et al., 1983).

Finally, our study could have been extended to the physiological and behavioural responses of handicapped-pair young as they represent the final level of parental investment. Because handicapped parents performed longer foraging trips, handicapped-pair chicks were less frequently provisioned during the guard stage (provisioning rate=1/foraging trip duration). Moreover, handicapped parents may have reallocated energy for their own maintenance and transferred the extra cost induced by the handicap to their offspring. To what extent handicapped-pair young present a lower body mass, an altered nutritional state and higher levels of corticosterone (known to affect begging behaviour) should be considered in future studies.

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PROLACTIN
AND THE REGULATION OF FORAGING TRIP DURATION
IN ADÉLIE PENGUINS

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(soumis)

ABSTRACT

Alternating short and long foraging trips has been proposed as an adaptive strategy allowing parents to conciliate care of young and self-maintenance, respectively. The balance between prolactin, favouring parental care, and corticosterone, favouring foraging activities, may regulate this strategy.

The aim of this study was to test whether prolactin and corticosterone levels were involved in the regulation of foraging trip duration. To do this, we measured these hormones in male and female Adélie penguins *Pygoscelis adeliae* under two different conditions (experimental and environmental) that lengthened foraging trip duration.

In the experimental procedure, contrary to males, the group of females who performed longer foraging trips also exhibited lower prolactin levels. Similarly, when environmental conditions forced penguins to forage longer, males and females exhibited lower prolactin levels. The decision to perform a short or a long foraging trip was related to the pre-trip prolactin levels in females. However, this relationship was not constant across years.

These results indicate that, contrary to corticosterone concentrations, prolactin levels were modulated according to foraging constraints and that long foraging trips were generally related to lower prolactin levels. The adjustment of prolactin levels may also precede the decision to perform a long or a short foraging trip in females. This suggests that penguins are able to favour self-maintenance, by increasing the duration of their foraging trips consecutively to a decrease in prolactin levels. However, this does not exclude a role in foraging strategies of other hormonal systems depending on environmental conditions.

Keywords: corticosterone, foraging, penguin, parental care, prolactin, seabird

INTRODUCTION

During the breeding period, parents have to devote a certain amount of energy for breeding at the expense of their own requirements. In species where young must be cared for and fed by adults (e.g. altricial birds), parental behaviour can be divided in two main components: care of young and foraging. Foraging is essential for the adult to rebuild its reserves and to bring food back to its offspring but competes with care of young since feeding and breeding areas are usually distant (Curlee & Beissinger 1995, Chastel & Kersten 2002) . To conciliate these two conflicting activities, an alternation between long foraging trips, favouring adult maintenance, and short foraging trips, favouring young feeding, has been proposed (Chaurand & Weimerskirch 1994, Weimerskirch et al 1994.1997, 1999, Ropert-Coudert et al. 2004). In biparental species like seabirds, where young need for a certain time the presence of one parent (to provide heat or defend them from predators), the decision to forage by one parent will mechanically force the other one to wait fasting on the nest. The possibility for the parent on the nest to refeed will be then conditioned by the decision of its partner to return to look after the young.

The breeding period is accompanied by a series of hormonal changes in parents, prompting some authors to propose that the compromise between young attendance and foraging may be mediated by hormonal levels (e.g. Lormée et al. 2000, Chastel et al. 2005, Angelier et al. 2008, Groscolas et al. 2008). In birds, the main hormone promoting parental behaviour is prolactin while corticosterone is known to trigger locomotion and foraging activity (Astheimer et al. 1992; Challet et al. 1995, Landys et al. 2006, Storey et al. 2006 Angelier et al. 2007). Prolactin induces and maintains avian parental behaviour (Buntin 1996) and has been described to increase feeding rate to the chicks (Buntin et al. 1991). In precocial birds (i.e. with independent chicks at hatching), prolactin secretion has been described to depend on tactile and visual stimuli from the eggs, the chicks and the incubating mate (Buntin 1996). In contrast, in altricial birds, prolactin secretion is considered as being poorly dependent of external stimuli (Hector & Goldsmith 1985, Hall 1986) and thus remains elevated from incubation until, at least, chicks become thermally independent (Vleck et al. 1999).

High and constant prolactin levels, poorly dependant of the contact with the egg or the chick, are thought to lead foraging birds to come back regularly to look after the chicks and thus provide constant parental care despite long absences to forage (Angelier & Chastel 2009). For instance, in emperor penguins *Aptenodytes forsteri* and in some tropical seabirds, it has been proposed that females, who spend more time at sea than males, may need higher prolactin levels to come back to the nest and maintain appropriate parental care (Lormée et al. 1999, 2000). In that case, long foraging trips should be related to high prolactin levels. Alternatively, long foraging trip may also be expected to be associated to low prolactin levels when considering body condition. Indeed, prolactin concentrations may be related to body condition (Criscuolo et al. 2003; O'Dwyer et al. 2006, Angelier & Chastel 2009) and the amount of reserves the birds were able to accumulate during foraging trips and thus to foraging efficiency and resource availability (O'Dwyer et al. 2006). Birds presenting a low body condition may exhibit low prolactin levels (O'Dwyer et al. 2006), redirecting their effort away from current reproduction in favour of their maintenance and survival. In that case, since long foraging trips favour adult self-maintenance and survival (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1997, 1999, Ropert-Coudert et al. 2004), they should be associated to low prolactin levels.

Because of the opposite effects of corticosterone on parental behaviour, prolactin levels have to be considered in the light of corticosterone concentrations (Angelier et al. 2009a). It is assumed that high corticosterone levels should redirect energy allocation from parental care to self-maintenance (see Wingfield et al. 1998). As a consequence, high corticosterone levels should be related to long foraging trips. However it has been also shown in the Adélie penguin *Pygoscelis adeliae*, that high corticosterone levels could be related to short foraging trips, therefore suggesting that corticosterone is more likely to redirect energy allocation towards current reproduction in this species (Angelier et al. 2008).

The aim of this study was to test whether prolactin and corticosterone levels could be involved in the regulation of foraging trip duration i.e. in the mediation of the conflict between nest attendance and foraging. To do this, we took into consideration two parameters which extended foraging trip duration of Adélie penguins. First, we tested whether different foraging abilities may be related to variations in hormonal levels. For this, we mimicked a difference of intrinsic foraging capacity between birds by equipping them with external handicaps (disrupting the streamlined shape of penguins) and we monitored them in parallel with unequipped control penguins. This procedure led to a 70% increase in the foraging trip duration of handicapped chick-rearing penguins (1.73 ± 0.08 d *vs.* 1.00 ± 0.02 d, Beaulieu et al. 2009a). Second, control penguins were monitored in two years showing contrasting sea-ice conditions and characterized by different foraging trip durations (1.01 ± 0.02 d (early sea-ice retreat) *vs.* 1.24 ± 0.04 d (late sea-ice retreat)), presumably because of a change in prey accessibility (Beaulieu et al. 2009b).

We expected hormonal levels to be related to foraging trip duration. For prolactin, two opposite hypotheses are conceivable: birds performing longer foraging trips may exhibit (1) higher prolactin levels, leading them to come back to the colony to look after the chicks (in that case, parents would give priority to current reproduction), (2) lower prolactin levels since the protracted foraging duration may be due to a lower foraging efficiency and birds should give priority to their self-maintenance rather than to their offspring. Similarly, high levels of corticosterone may (1) favour current reproduction and thus be related to short foraging trips, or (2) give priority to self-maintenance and thus be related to long foraging trips

METHODS

This study was approved by the ethic committee of the French Polar Institute Paul Emile Victor. It took place in Dumont d'Urville (66°40'S, 140°01'E), Adélie Land, Antarctica in austral summers 2006-07 and 2007-08. In 2006-07, sea-ice retreated 3 months earlier than in 2007-08

Handicap procedure

In 2006-07, 92 individuals belonging to 46 pairs were randomly selected for the experimental study. A few days before egg laying, the birds were individually marked for identification with a subcutaneous transponder and a letter painted on their chest with Nyanzol-D (Fig. 1). Sex was determined *a posteriori* by using a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962, Kerry et al. 1993).

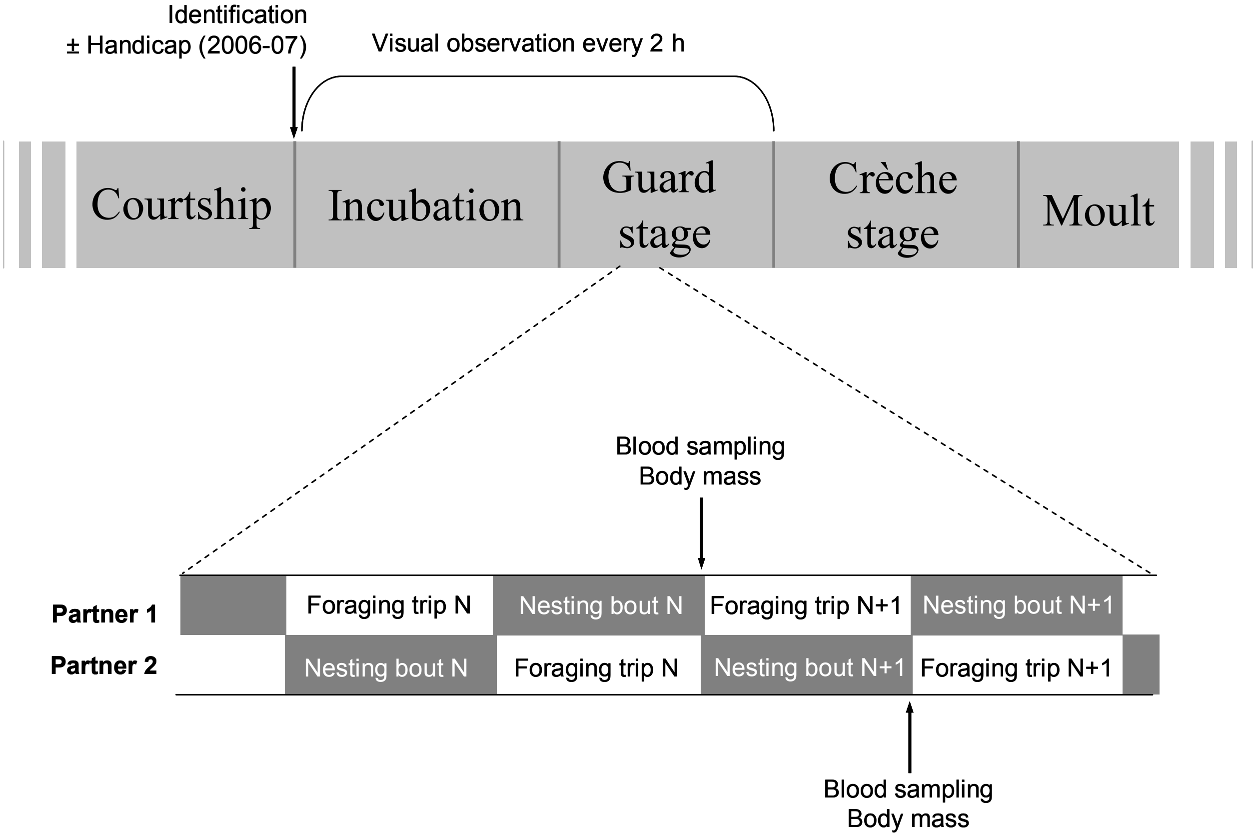

Fig. 1: Breeding cycle of Adélie penguins with emphasis on study protocole depicting blood sampling and body mass determination according to foraging trips and nesting bouts.

Foraging behaviour was manipulated by equipping one bird per pair (n=30 birds) with a large dummy Plexiglas device attached with mastic, cyanoacrylate glue, Tesa tape and cable ties to the middle-back feathers (Wilson et al 1997, Beaulieu et al. 2009a). In total, 16 pairs were assigned to the control group (where none of the mates was equipped), 13 pairs to the handicapped-female group (where only the females were equipped) and 17 pairs to the handicapped-male group (where only the males were equipped). We distinguished three groups at the pair level (control, handicapped-female and handicapped-male pairs) each constituted by males and females, therefore resulting in six groups at the parent level (control females, control males, handicapped females and their male partners, handicapped males and their female partners).

Interannual variability

Control birds, electronically-identified by transponders, were also followed the subsequent season. They were visually identified as described above and the sex determination carried out in 2006-07 was entirely confirmed in 2007-08.

During the two breeding seasons, nests were visually observed from the distance every two hours to monitor the departure to the sea and the return from foraging of each bird (Fig. 1). The durations of nest attendance and foraging trips were then calculated.

Blood sampling

Birds rearing young were captured and weighed with an electronic balance (Ohaus, ± 2 g) during the guard stage (i.e. when constant nest attendance by one parent is required), 40-45 days after egg laying, when chicks were about 10 days old and when prolactin concentrations had reached a high stable plateau (Vleck et al. 1999). This operation occurred after a nest relief and just before the penguin left the colony to forage at sea (Fig. 1). Blood was collected from the wing vein with a heparinized syringe within five minutes following the bird capture, so that handling time will not to affect baseline corticosterone and prolactin levels (Vleck et al. 2000, Chastel et al. 2005). After centrifugation, plasma samples were quickly stored at -20°C. Blood sampling depended on the bird departure and therefore occurred at any time of the day. However no daily rhythm of prolactin or corticosterone secretion has been reported in Adélie penguins (Vleck et al. 2002, Angelier et al. 2008).

In the experimental procedure, we were able to collect blood on 72 chick-rearing birds to measure both corticosterone and prolactin concentrations. To conduct strict interannual comparison of hormonal levels and to avoid any potential bias linked to pair instability on hormonal level (Angelier et al. 2007), we selected within control birds, individuals who returned to the colony to breed with the same partner and were still breeding during the guard stage in 2006-07 and 2007-08 (10 stable control pairs).

Laboratory analyses

Analyses of prolactin were carried out at the Centre d'Etudes Biologiques de Chizé (CEBC, France) and concentrations were determined by heterologous radioimmunoassay as validated for penguins (Cherel et al. 1994, Lormée et al. 1999). Corticosterone levels were determined by immunoassay (Assay Pro, AssayMax Corticosterone ELISA Kit) at the IPHC-DEPE, France. Intra and inter assay variation were 8% and 9% respectively, for prolactin measurements, and 5% and 7% respectively, for corticosterone measurements.

Statistical analyses

We performed comparisons between control and handicapped penguins with a general linear model including the treatment (control *vs.* handicapped), the sex and their interaction as fixed factors. To compare hormonal levels between years, we used a general linear mixed model with the year (repeated factor), the sex and their interaction as fixed factors and the individual as a random factor. To obtain normality of residuals (Shapiro-Wilk test), prolactin data were log-transformed.

To determine the cause-and-effect relationships between hormonal levels, body mass and the durations of foraging trips and nest attendance, we also conducted in control birds, Pearson or Spearman correlations (according to normality of data) between hormonal levels (prolactin and corticosterone concentrations), body mass and the duration of the previous foraging trip, the time spent on the nest before blood sampling and the duration of the foraging trip following blood sampling (Fig. 1). We conducted these correlations for control males and females (stable and unstable) for which we had all the considered parameters (nesting/foraging durations, body mass, hormonal levels).

Analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, Ill., USA). Results are expressed as means ± SE and significance level was set at $\alpha=0.05$.

RESULTS

Effects of experimental treatment

Corticosterone levels were more than 2-fold higher in males than in females (3.10 ± 0.37 ng/mL and 1.40 ± 0.38 ng/mL, respectively; $F_{1, 66}$=10.14, P=0.002). In contrast, prolactin levels were 38% lower in males than in females (96.12 ± 3.62 ng/mL and 155.76 ± 11.12 ng/mL, respectively; $F_{1, 66}$=33.72, P<0.001). Hormonal levels were not influenced by the treatment (corticosterone: $F_{2, 66}$=0.54, P=0.59, prolactin: $F_{2, 66}$=0.35, P=0.70) and the interaction sex*status was not significant for corticosterone ($F_{2, 66}$=0.41, P=0.66). However this interaction was significant for prolactin ($F_{2, 66}$=4.35, P=0.02) with handicapped females exhibiting 31% lower prolactin levels than control females (P=0.048). Prolactin levels were similar between control females and females with a handicapped male females and between male groups (all P>0.05, Fig. 2).

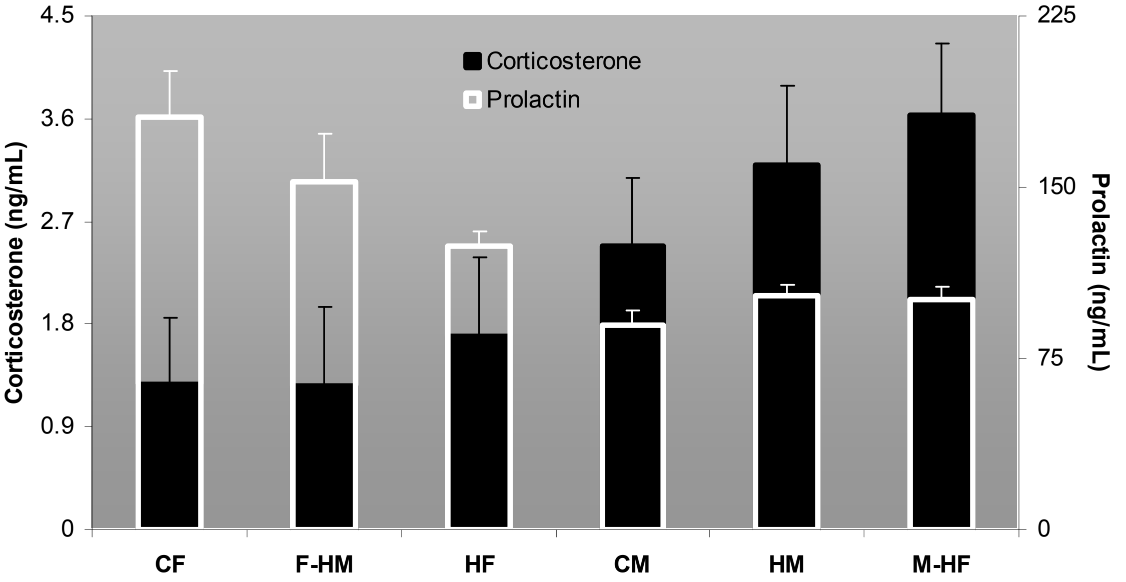

Fig. 2: Plasma corticosterone and prolactin levels in control females (CF), handicapped-male females (=partner females, F-HM), handicapped females (HF), control males (CM), handicapped-female males (=partner males, M-HF) and handicapped males (HM) in 2007.

Interannual variability

Considering the two years, males and females had similar corticosterone levels ($F_{1, 17}$=1.30, P=0.26, Fig. 3) but females exhibited 34% higher prolactin levels than males (125.95 ± 11.73 ng/mL and 82.87 ± 5.96 ng/mL, respectively; $F_{1, 17}$=17.41, P=0.001). On average, corticosterone levels were similar between the two years ($F_{1, 17}$=1.35, P=0.25). In contrast, prolactin concentration was 29% lower in 2007-08 than in 2006-07 (early sea-ice retreat, $F_{1,}$

$_{17}$=10.66, P=0.005). The interaction sex*year was not significant for corticosterone ($F_{1,\ 17}$=0.20, P=0.66) or prolactin ($F_{1,\ 17}$=0.32, P=0.58, Fig. 3).

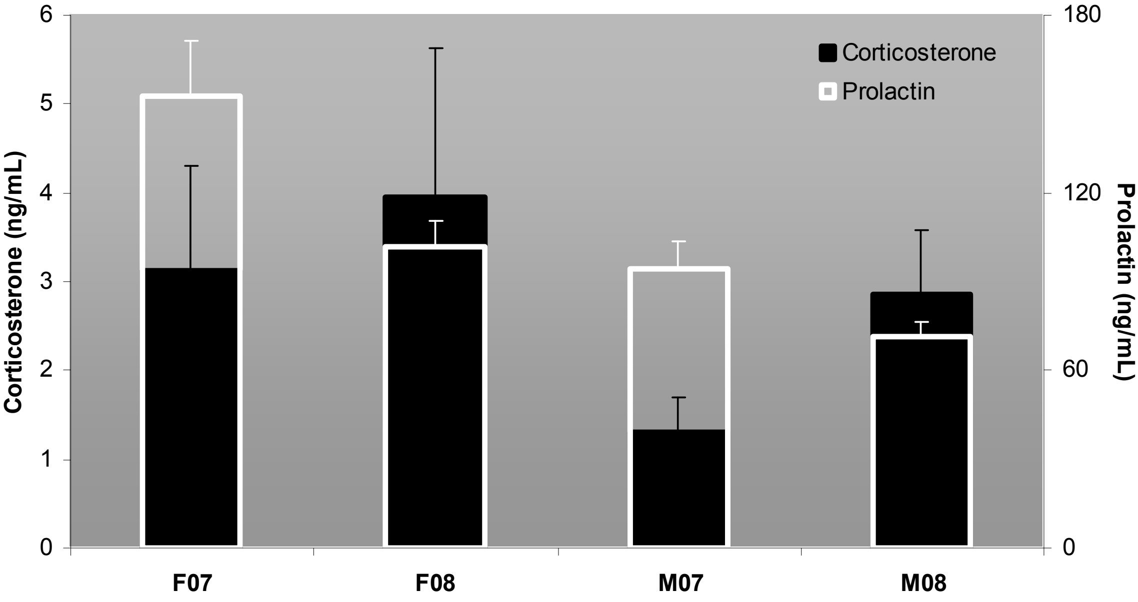

Fig. 3: Plasma c orticosterone and prolactin levels in females (F) and males (M) in 2007 and 2008.

Correlation between hormonal levels, body mass and brooding / foraging duration in control birds

The durations of the foraging trip before blood sampling ranged from 0.77 to 2.03 days in females and from 0.55 to 1.64 days in males (considering 2007 and 2008). They did not correlate with corticosterone or prolactin levels (Table 1). In 2007, in females, prolactin levels were negatively correlated with the duration of the foraging trip following blood sampling (0.81-1.31 days, Table 1). In contrast, corticosterone concentrations never covaried with foraging trip duration either in females or in males (Table 1, Fig. 4). In 2007, in males, corticosterone levels were however positively correlated with the time spent on the nest before blood sampling (0.49-1.67 days; Table 1, Fig. 4).

In 2008, female body mass (3.51-4.60 kg) was positively correlated with prolactin but not with corticosterone levels. In contrast, male body mass (3.89-5.05 kg) was negatively correlated with corticosterone but not with prolactin levels (Table 1). None of these relationships were found in 2007.

Table 1: Correlations between hormonal levels, body mass and nesting/foraging durations in female and male Adélie penguins in 2007 and in 2008.

			Foraging trip N		Time on the nest		Body mass		Foraging trip N+1	
			r	P	r	P	r	P	r	P
2007	Females (n=13)	Corticosterone	0.22^{s}	0.46^{s}	-0.32^{s}	0.28^{s}	0.26^{s}	0.38^{s}	-0.21^{s}	0.49^{s}
		Prolactin	0.18^{p}	0.55^{p}	0.15^{p}	0.63^{p}	0.13^{p}	0.74^{p}	**-0.70**^{p}	**0.008**^{p}
		Body mass	0.29^{p}	0.35^{p}	0.35^{p}	0.24^{p}			0.01^{p}	0.99^{p}
	Males (n=14)	Corticosterone	-0.19^{s}	0.51^{s}	**0.73**^{s}	**0.003**^{s}	0.21^{s}	0.48^{s}	0.20^{s}	0.49^{s}
		Prolactin	0.16^{p}	0.58^{p}	-0.41^{p}	0.15^{p}	-0.24^{p}	0.42^{p}	-0.32^{p}	0.26^{p}
		Body mass	-0.33^{p}	0.26^{p}	-0.06^{p}	0.85^{p}			-0.37^{p}	0.20^{p}
2008	Females (n=10)	Corticosterone	0.05^{s}	0.90^{s}	-0.01^{s}	0.99^{s}	0.50^{s}	0.14^{s}	-0.06^{s}	0.88^{s}
		Prolactin	0.04^{p}	0.92^{p}	-0.09^{p}	0.80^{p}	**0.70**^{p}	**0.03**^{p}	-0.08^{p}	0.84^{p}
		Body mass	-0.14^{p}	0.73^{p}	-0.21^{p}	0.56^{p}			-0.18^{p}	0.61^{p}
	Males (n=10)	Corticosterone	0.38^{s}	0.28^{s}	-0.29^{p}	0.42^{p}	**-0.72**^{p}	**0.02**^{p}	0.42^{p}	0.22^{p}
		Prolactin	0.57^{s}	0.09^{s}	0.05^{p}	0.89^{p}	-0.30^{p}	0.40^{p}	-0.32^{p}	0.37^{p}
		Body mass	-0.46^{s}	0.18^{s}	0.14^{p}	0.69^{p}			-0.61^{p}	0.06^{p}

^{s} Spearman correlation, ^{p} Pearson correlation. Significant results are in bold

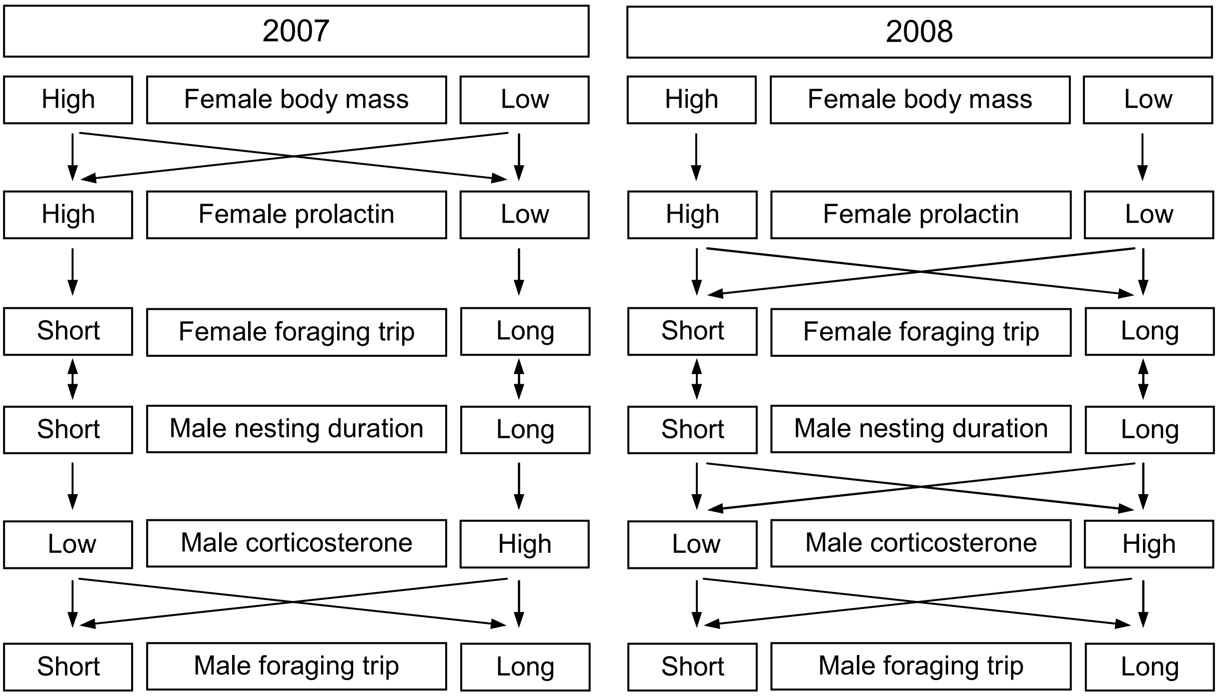

Fig. 4: Relationships between body mass, hormonal levels and nesting/foraging periods in females and males in 2007 and in 2008. For clarity, male body mass is not represented here (see table 1).

DISCUSSION

Overall our results indicate that prolactin levels are not fixed and are more sensitive than corticosterone levels to foraging constraints in Adélie penguins. As corticosterone was never modified by foraging constraints in our study, it does not seem to be involved in the trade-off between foraging behaviour and nest attendance. In contrast, prolactin levels were related to foraging trip duration and seems more likely to be involved in this trade-off. As observed in emperor penguins (Lormée et al. 1999), female Adélie penguins exhibit higher prolactin levels while performing longer foraging trips (Clarke et al. 1998). As a consequence of this observation, one may assume that higher prolactin levels are essential for birds to come back to the colony after a long foraging trip. In contrast, we found that, under experimental or environmental constraints obliging Adélie penguins to perform longer foraging trips, prolactin levels generally decreased. Low prolactin levels favouring long foraging trips appear consequently to give priority to self-maintenance. However these low prolactin levels also changed the balance between corticosterone and prolactin in favour of corticosterone. As a consequence, even though no relationship between foraging behaviour and corticosterone has been highlighted in this study, high corticosterone levels relatively to prolactin levels may also be considered to be related to long foraging trips.

The unmodified prolactin levels found in partner birds confirmed the independence of prolactin levels with chick contacts, as expected in altricial birds (Hector & Goldsmith 1985, Hall 1986). Indeed, partner birds spent more time in contact with the chicks because of the protracted foraging trips of their handicapped mates. Nevertheless, they did not exhibit higher prolactin levels, suggesting that in Adélie penguins, prolactin levels are not dependent on the time spent in contact with the young. This trend was also confirmed by prolactin levels in control penguins that never correlated with the time spent on the nest with chicks.

The regulation of the prolactin/corticosterone balance seems to be sex-specific in the experimental procedure: females had higher prolactin levels than males and males had higher corticosterone levels than females. Handicapped females, performing longer foraging trips, were more prone than males to adjust prolactin levels according to foraging constraints. In addition, the more important contribution of prolactin in the regulation of foraging trip duration in females was reinforced by the significant correlations found in control females (but not in males) between prolactin levels and the duration of the foraging trip following blood sampling (in 2007).

Prolactin levels were not correlated with the duration of the foraging trip before blood was sampled. Even though prolactin levels have been described to be as high after as before a foraging trip (Hector & Goldsmith 1985, Hall 1986) or before and after feeding chicks (Garcia et al. 1996), we cannot rule out that prolactin levels changed along one bout of nest attendance and that blood sampling was carried out too late (1-2 day(s) in the current study) after the bird returned to reflect the characteristics of the previous foraging trip.

In contrast to the previous foraging trip, prolactin levels were negatively correlated with the duration of the foraging trip following blood sampling in control females in 2007. These data show that the adjustment of prolactin levels preceded the decision to perform a short or a long foraging trip (Fig. 4). A quite similar relationship had also been highlighted in meerkats *Suricata suricatta* where low prolactin levels lead adults to forage (Carlson et al. 2006). Moreover, in 2007, corticosterone levels were positively correlated with the time spent by males fasting on the nest (i.e. the duration of the female foraging trip, Fig. 1), highlighting the interdependence between the prolactin levels in females and the corticosterone concentrations in males (Fig. 4). However this interdependence does not seem to be valid in handicapped penguins. Indeed, lower prolactin levels in handicapped females were not associated to significantly higher concentrations of corticosterone in their partners, despite a visual trend (see Fig. 2).

The anticipatory prolactin levels before foraging in females was not constant since it was not found across years. Indeed, in 2008, prolactin levels did not correlate with foraging trip duration but with body mass in females (Fig. 4). This strongly suggests that parental behaviours can be related to certain hormonal status depending on environmental conditions (Fig. 4). For instance, Angelier et al. (2008) found that Adélie penguins in Dumont d'Urville, during the guard stage in 2005, regulated the duration of their foraging trip according to their pre-trip corticosterone levels, with penguins exhibiting low corticosterone levels performing longer foraging trips. We did not find a similar trend during the guard stage of Adélie penguins in 2007 and in 2008 at the same location: long foraging trips were not related to low pre-trip corticosterone levels but were related to low pre-trip prolactin levels in females in 2007. This suggests that to redirect energy allocation from parental care to self-maintenance through long foraging trips, Adélie penguins can use two alternatives: low pre-trip corticosterone levels (Angelier et al. 2008) or low pre-trip prolactin levels (this study) according to environmental conditions.

Overall our results show that prolactin is more sensitive to foraging constraints than corticosterone. However this apparent higher sensitivity of prolactin may be due to a difference in the persistence of the prolactin and corticosterone responses to the different foraging constraints. For instance, we cannot rule out that corticosterone levels had also increased but only temporarily before returning to lower levels (when blood was sampled) since high corticosterone levels are not physiologically sustainable on the long term (Romero 2004). Indeed, Angelier et al. (2009b) found in the black-legged kittiwake *Rissa tridactyla* that a short-term corticosterone increase was accompanied by a persistent 30% decrease in prolactin levels. To what extent, the observed lower prolactin levels found in our study resulted from a temporary increase of corticosterone levels remains to be investigated in further studies including the kinetic aspects of hormonal secretion. Finally, to go further than our correlative results, experimental manipulations of prolactin and corticosterone would be worthwhile to elucidate the causal relationships between hormonal levels and foraging strategies.

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Article 7 : Statut oxydant et contrainte expérimentale

CONTROLLING FOR OXIDATIVE STRESS AND SAVING TELOMERE LENGTH: MECHANISMS TO AVOID THE FITNESS COST OF REPRODUCTION IN LONG-LIVED BIRDS?

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(soumis)

ABSTRACT

Life-history theory predicts that high reproductive investment alters self-maintenance and reduces the probability of successful future breeding attempts. Several mechanisms underlying the cost of reproduction have been previously suggested, but how parental effort may impact cell and organism senescence remains largely unknown. The effects of oxidative stress - the unbalance between oxidative damage and defences – on telomere dynamics may underlie this relationship. Indeed, oxidative stress is associated to costly activities like breeding and impacts telomere dynamics that are known to predict survival in birds. Long-lived species, expected to minimize the adverse effects of current reproduction on their body maintenance, should therefore control their oxidative stress and preserve their telomeres whatever the breeding workload. In the present paper, we tested this hypothesis by determining experimentally how the oxidative balance and telomere length are modified when long-lived Adélie penguins (*Pygoscelis adeliae*) face a costly reproductive event. In agreement with the hypothesis postulating that long-lived species should prioritize their self-maintenance, Adélie penguins increase their antioxidant defences when experiencing a high breeding effort. This adaptability resulted in no acceleration in telomere loss reflecting no impact on organism senescence. While previous studies have shown that long-lived species favour self-maintenance when breeding constraints increase, our study is the first to point a cellular mechanism likely to explain how this may occurs, thereby suggesting that the couple oxidative stress / telomere is an essential mediator of life-history strategies.

Keywords: life history theory, long-lived species, oxidative stress, telomeres

INTRODUCTION

Life-history theory postulates that individuals have to allocate limited resources into competing life functions (Stearn 1992). Because of this energetic conflict, living beings have to face trade-offs and may be constrained to reallocate resources to a given function at the expense of another one under specific circumstances. The trade-off between reproduction and self-maintenance represents the best illustration of this allocation conflict, with an increased allocation in breeding effort being associated with a subsequent lower fecundity or survival (Gustafsson & Pärt 1990, Reed et al. 2008). However, even though many studies focused on the reproduction and survival conflict (e.g. Sanz et al. 2000, Golet et al. 2004, Paredes et al. 2005, Navarro & Gonzáles-Solís 2007), we still only have a rough idea about the nature of the underlying physiological mechanisms. To buffer the deleterious effects of increasing reproductive demands on self-maintenance, adults can modulate five physiological components: secretion of hormones with pleiotropic effects, intermediate metabolism and fuel allocation, immune function, mating costs and defense against stress (reviewed in Harshman & Zera 2007). Ultimately, some of these physiological processes are likely to act directly and negatively on subsequent fecundity and longevity by accelerating ageing rates (Partridge & Gems 2006).

In this context, one proximal factor that has been recently explored is oxidative stress i.e. the unbalance between the production of reactive oxygen species (ROS) and the antioxidant capacity of the organism (Finkel & Holbrook 2000). ROS production results from mitochondrial metabolic processes that consume oxygen and may damage proteins, lipids and DNA and generate reactive oxygen metabolites (ROM). To overcome this potential damage, living organisms are able to raise an antioxidant barrier, constituted by exogenous diet-derived (e.g. vitamin C, E, carotenoids) and endogenous (e.g. uric acid, superoxide dismutase, glutathione peroxidase) molecules converting ROS into less reactive molecules (Vleck et al. 2007, Cohen & McGraw 2009). As a result, antioxidant levels are expected to track ROS production. As stated by the metabolic rate/free radical theory of aging, metabolic rate is inversely correlated to lifespan (Wiersma et al. 2007), because a higher metabolic rate (e.g. when the breeding effort is increased) is related to a higher oxygen consumption and a higher ROS production (Harman 1956, Beckman & Ames 1998). In the short-lived zebra finch *Taeniopygia guttata*, it has been shown that reproduction decreases antioxidant defences, illustrating that oxidative stress may mediate the cost of reproduction (Alonso-Alvarez et al. 2004, Wiersma et al. 2004). In addition, besides its implication in reproduction, resistance to oxidative stress has also been related to higher survival rates in male alpine swifts *Apus melba* (Bize et al. 2008). Oxidative stress therefore appears as an important mediator between reproductive effort and the probability to survive and to reproduce.

The link between oxidative stress and self-maintenance may be explained by the deleterious effects of free radicals on key biological molecules (i.e. oxidative damage), which are considered as the principal proximate mechanism explaining cell senescence (Beckman & Ames 1998). Oxidative stress triggers cell death *via* membrane damage (cell necrosis) or by activating pro-apoptotic cellular pathways (Finkel 2003). This activation may be triggered by the disruption of DNA chromosome end structures: the telomeres (von Zglinicki 2002). Telomeres are well conserved non-coding sequences of a repeated motif $(T_2AG_3)_n$ that cap the ends of chromosomes and stabilise the genome (see Monaghan & Haussmann 2006). Telomeres shorten because of the end-replication problem of the 5'→3' template strand (Blackburn 1991), but this erosion can be accelerated by different stress factors (Epel et al. 2004) among which oxidative stress (von Zglinicki 2002, Richter & Von Zglinicki 2007). Once telomere length reaches a critical lower threshold in absence of appropriate maintenance responses (Blackburn 2000), replicative senescence and apoptosis occur. As a result, telomere length can be used at the organism level, as an index of the biological (rather than chronological) age, "indicative of the current position of the individual in its journey through life" (Monaghan & Haussmann 2006). Therefore, telomere dynamics (the rate at which telomere sequences are lost with time) has been used in ecological studies focusing on life history trade-offs in wild animal populations (Haussmann 2000, Pauliny et al. 2006) and has recently been described as a better predictor of adult survival than age in a wild population of alpine swifts (Bize et al. 2009) or in free-living corvids (Salomons et al. 2009). Therefore, if individuals with short telomeres are less likely to survive, acceleration of telomere shortening rate, after a costly breeding event, may be a good candidate to explain how current reproduction alters adult self-maintenance and survival. However, there are no studies to date that experimentally tested whether increased breeding effort actually modify telomere dynamics.

Even though much evidence is now accumulating on the implication of oxidative stress in the trade-off between reproduction and self-maintenance, most of the work has been done on passerines (Alonso-Alvarez et al. 2004, Wiersma et al. 2004), these short lived birds compromising oxidative defenses when facing increased reproduction workload. According to evolutionary theory, long-lived birds should avoid long-term impact on adult survival and therefore sacrifice current reproduction and prioritize self-maintenance. Accordingly, long-lived birds should exhibit a higher oxidative defense to respond to the increased breeding effort and ROS production, and no acceleration in telomere loss should be detected.

To test this hypothesis, the breeding effort of adult Adélie penguins (*Pygoscelis adeliae*) was modified by increasing the cost of foraging, which is the most costly breeding activity in this species (Chappell et al. 1993). We increased breeding constraints by reducing the hydrodynamic properties and therefore the foraging efficiency of these streamlined animals. As expected, handicapped penguins provided a higher effort while foraging at sea than control birds since they performed 70% longer foraging trips (1.73 ± 0.08 d and 1.00 ± 0.02 d during chick rearing) and lost 60% more body mass (Beaulieu et al. 2009). The impact of parental workload level was followed in a longitudinal study implying repeated blood and fitness measurements on the same individuals. During the subsequent breeding season, the lower resight rate of handicapped males and the lower fecundity of handicapped females (Beaulieu et al. 2009) indicated that the handicap procedure induced a cost of reproduction in the experimental penguins. Provided that handicapped penguins exhibited a higher breeding effort, we expected their production of ROS to be increased. These birds may then show either (i) higher rates of telomere shortening or (ii) enhanced antioxidant capacities to buffer any deleterious impact on telomeres. According to life history of long-lived animals (Stearns 1992), we predict that long-lived Adélie penguins should set-up efficient antioxidant networks that will favour adult maintenance.

MATERIAL AND METHODS

Fieldwork

The study took place in Dumont d'Urville (66°40'S; 140°01'E), Adélie Land, Antarctica during austral summers 2006-07 and 2007-08.

In 2006-07, at the end of the courtship period, 46 pairs of Adélie penguins were identified with a subcutaneous transponder and a symbol painted on their chest feathers with Nyanzol-D. Among them, 30 were equipped with a large dummy device (25x35x60 mm, 60 g), attached to the middle-back feathers to increase the cost of foraging. Diving behaviour of instrumented penguins is considered to be altered if the cross sectional area (CSA) of the equipment represents >1% of the animal's CSA (Culik & Wilson 1991). Here penguins were handicapped with instruments representing ~4% of their CSA; this size was selected not to be too disadvantaging (see Beaulieu et al. 2009). The remaining 15 pairs were used as controls. Birds were captured a second time during the breeding season while rearing chicks (40-45 days after laying), after a nest relief and just before leaving the colony to forage at sea. Sex was determined *a posteriori* by using a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962, Kerry et al. 1993).

In 2007-08, at the end of the courtship period, all the nests of the colony were checked with a hand held antenna to find experimental birds identified with a transponder the previous year. At the very beginning of incubation, the number of eggs was checked in every nest.

Blood was collected from the wing vein with a heparinized syringe just after each capture, i.e. before treatment (courtship period in 2006-07), during treatment (chick rearing 2006-07) and after treatment (courtship 2007-08, Fig. 1). After centrifugation, plasma and red blood cells were separated in Eppendorf tubes and stored at -20°C until laboratory analyses.

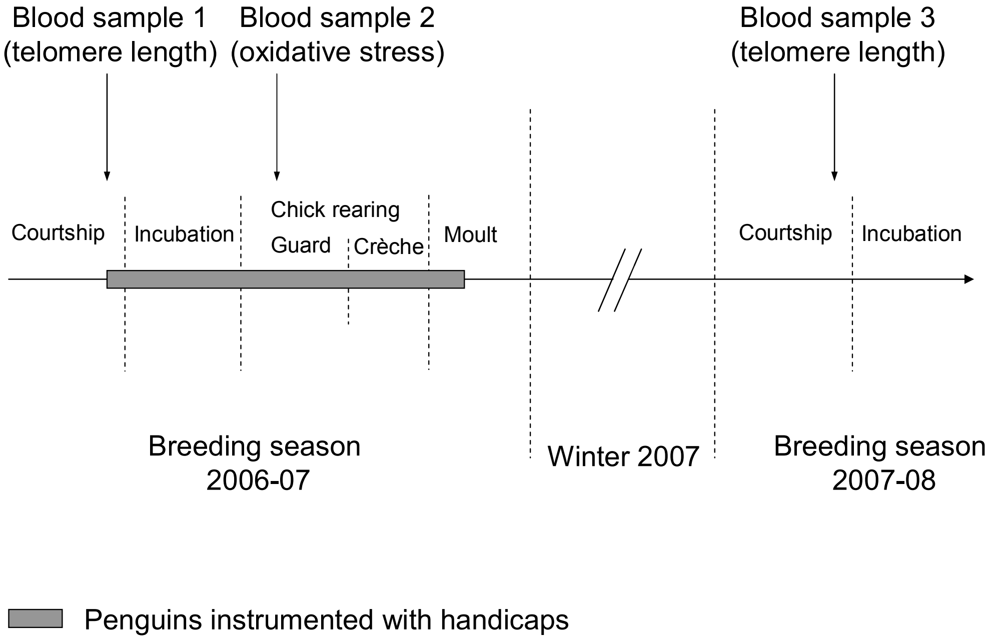

Fig. 1: Consecutive breeding cycles of Adélie penguins in 2006-07 and 2007-08 and study protocol. The grey area represents the period when penguins were instrumented.

Laboratory analyses

Analyses of oxidative stress and telomere length were carried out at the IPHC-DEPE, France. To measure oxidative stress on plasma samples collected during treatment, we used the d-ROMs test and the OXY-ADSORBENT tests (Diacron International). The d-ROM test measures the concentration of hydroperoxyde, a ROM resulting from the attack of ROS on organic substrates, while the OXY-ADSORBENT test measures the total antioxidant barrier of plasma (for details on the procedure, see Costantini & Dell'Omo 2006, Costantini et al 2006). These tests are now widely used in medical investigation (e.g. Christou et al. 2003, Markoulis et al. 2006, Vassalle et al. 2008).

DNA was extracted from 5 µL of red blood cells using a commercial kit (DNeasy® Blood & Tissue kit, Qiagen). Telomere measurements were conducted following the procedure described by Criscuolo et al. (2009) and already used by Bize et al. (2009). Quantitative real-time amplification (qPCR) of the telomere sequence, initially set-up on humans (Cawthon 2002), has been adapted to birds (Criscuolo et al. 2009). Briefly, this method is based on the measurement of a number of amplification cycles necessary to detect a lower threshold of fluorescent signal, the cycle number being proportional to the telomere length (T), or to the length of a control gene (S). A ratio (*T/S*) of telomere repeated copy number (*T*) to single control gene copy number (*S*) is then calculated for each sample that will reflect relative inter and intra-individual differences in telomere length. For a detailed description of the analysis of qPCR results, refer to Criscuolo et al. (2009). As a single control gene, we used *Pygoscelis adeliae* zinc finger protein (ZENK, Chubb 2002), the primer sequences being defined using Primer 3 software (Adel1: 5'-CAACTGCCGTTTAAGTTTTCC-3'; Adel2: 5'-AATATGGCCCTGCAAATTCC-3'). Primer sequences for telomere amplification were Tel1b (5'-CGGTTTGTTTGGGTTTGGGTTTGGGTTTGGGTTTGGGTT-3') and Tel2b (5'-GGCTTGCCTTACCCTTACCCTTACCCTTACCCTTACCCT-3'). Telomere and control gene PCR conditions were 10 min at 95°C followed by 30 cycles of 30 s at 56°C, 30 s at 72°C and 60 s at 95°C. qPCR amplicon sizes were determined after electrophoresis on a 1.5 % agarose gel run in standard TBE buffer (90 V for 10 min and 130 V thereafter) and using ethidium bromure staining (Fig. 2). Amplification of zinc finger protein gene led to a product size of the expected 250 kb, predicted by primers alignment of the ZENK gene sequence. Telomere amplification produced a smear of several amplicons with a darker band between 50 and 100 kb, the lowest predicted size given by the primer sequences (78 kb, Cawthon 2002), the amplification of this shortest amplicon being proportional to the total sample telomere length. Telomere and ZENK real-time amplifications were carried out in duplicate on each plate and twice on two different plates and the mean values of the four measurements of telomere and control gene were used to calculate the final T/S ratio for each sample. Mean coefficient of variation was 2.92% for the telomere essays and 2.21% for ZENK essays. Telomere shortening was obtained on one-year scale, by subtracting the telomere length after treatment to the telomere length before treatment (Fig. 1).

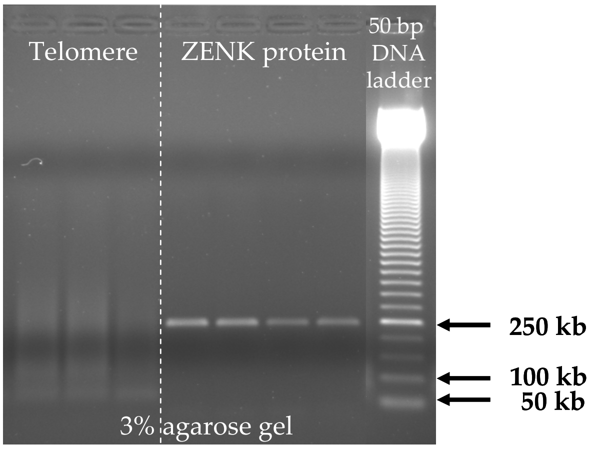

Fig. 2: Agarose gel electrophoresis of qPCR products from telomere (left) and control gene (zinc finger (ZENK) protein gene, right). Twenty microliters of PCR products of three (telomeres) and four (control gene) different samples were loaded into each lane of a 1.5% agarose gel. Band visualisation has been obtained using ethidium bromide after UV exposition. The PCR products of the telomere amplification migrate to the expected 78-bp region, those of the control gene to the 250 bp region.

Laboratory analyses were carried out on 15 birds from the control group and 17 birds from the handicapped group.

Statistical analysis

Male and female Adélie penguins allocate energy differently in reproduction: males' metabolic expenditure is higher than that of females over the breeding season but the reproductive effort associated with feeding chicks is lower in males than in females (Chappell et al. 1993). Moreover the inter-annual survival is higher in males than in females after a breeding attempt (Ainley & DeMaster 1980, Dugger et al. 2006). For these reasons, we could expect that oxidative stress and telomere dynamics to be sex-biased in Adélie penguins. Consequently the factor "sex" was considered in every statistical model.

To analyse the oxidative damage, the antioxidant barrier and the telomere shortening, we used general linear models with the sex, the treatment (control or handicapped) and their interaction as fixed factors. In addition, we assessed the influence of the initial telomere length on oxidative damage, antioxidant barrier and telomere shortening with Pearson correlations. When initial telomere length covaried with a parameter, it was added as a covariate in the model. We excluded from these analyses, birds that began but failed to breed in 2006-07 (n=1 control female, n=1 handicapped female, n=3 handicapped males) since they did not return to the colony during the breeding season once unsuccessful (blood sample 2 missing, Fig. 1). However, the 32 birds were taken into consideration to compare initial telomere length between groups (blood sample 1, Fig. 1). In addition, we conducted linear regressions with clutch size in 2007-08 as an independent factor and oxidative status in 2006-07 and telomere dynamics as dependent factors.

Normality was assessed with a test of Shapiro-Wilk and all analyses were conducted using SPSS 16.02 (SPSS Inc.). Results are expressed as means ± SE and significance level was set at α=0.05.

RESULTS

Oxidative stress

Plasmatic ROM levels measured in adult penguins in the breeding season 2006-07 were similar between males and females (5.60 ± 0.41 and 6.03 ± 0.39 mg H_2O_2/dL, respectively; $F_{1, 23}$=0.60, P=0.45). We did not find any differences between handicapped and control birds (5.75 ± 0.41 and 5.88 ± 0.39 mg H_2O_2/dL, respectively; $F_{1, 23}$=0.05, P=0.82, Fig. 3 A) and the interaction sex*treatment was not significant ($F_{1, 23}$=1.37, P=0.25). Similarly, males and females exhibited the same antioxidant plasmatic levels in 2006-07 (255 ± 15 and 275 ± 14 mmol-1 HOCL neutralised, respectively; $F_{1, 23}$= 0.95, P=0.34). However, handicapped penguins displayed 35% higher antioxidant levels than controls (305 ± 15 and 226 ± 14 mmol-1 HOCL neutralised, respectively $F_{1, 23}$= 14.74, P=0.001, Fig. 3 B). There was no interaction sex*treatment ($F_{1, 23}$= 0.30, P=0.59).

Initial telomere length

There was no correlation between initial telomere length and our two measurements of oxidative status, i.e. plasmatic ROM (r=-0.16, n=27, P=0.42) or antioxidant barrier levels (r=-0.02, n=27, P=0.92).

Among the 32 birds captured during courtship 2006-07, females had 35% shorter telomeres than males (*T/S* ratio: 1.25 ± 0.14 and 1.68 ± 0.14, respectively, $F_{1, 28}$=4.61, P=0.04) and there was no significant differences in telomere length between handicapped and non-handicapped animals in 2006-07 (treatment: $F_{1, 28}$= 0.65, P=0.43, sex*treatment: $F_{1, 28}$=2.70, P=0.11). Considering the 27 birds rearing chicks, the trends concerning initial telomere length were the same (sex: $F_{1, 23}$= 3.69, P=0.07, treatment: $F_{1, 23}$= 0.29, P=0.60, sex*treatment: $F_{1, 23}$=2.71, P=0.11), all groups starting then the experiment with the same mean relative telomere length. Initial telomere length was related to the rate of telomere loss between the two years of reproduction: for all birds, initial telomere length was negatively correlated with the rate of telomere shortening (r=-0.82, n = 27, P<0.001), birds having the longest telomeres in 2006-07 being also those losing more telomere repeats between 2006-07 and 2007-08. Initial telomere length was then used as a covariate for the subsequent statistical tests.

Telomere shortening

Rate of telomere shortening was evaluated between the two breeding years 2006-07 and 2007-08 in handicapped and control birds. Initial telomere length had a strong effect on telomere shortening between the two years ($F_{1, 21}$= 29.96, P<0.001). Telomere shortened similarly between the two years in males and females (-0.19 ± 0.10 *vs.* -0.10 ± 0.09 T/S, respectively; $F_{1, 21}$= 0.45, P=0.51) and birds from both experimental groups exhibited similar rates of telomere loss (-0.13 ± 0.10 *vs.* -0.16 ± 0.09 *T/S* in handicapped and control penguins, respectively; $F_{1, 21}$= 0.03, P=0.87, Fig. 3 C). The interaction sex*treatment was not significant ($F_{1, 21}$= 1.82, P=0.19).

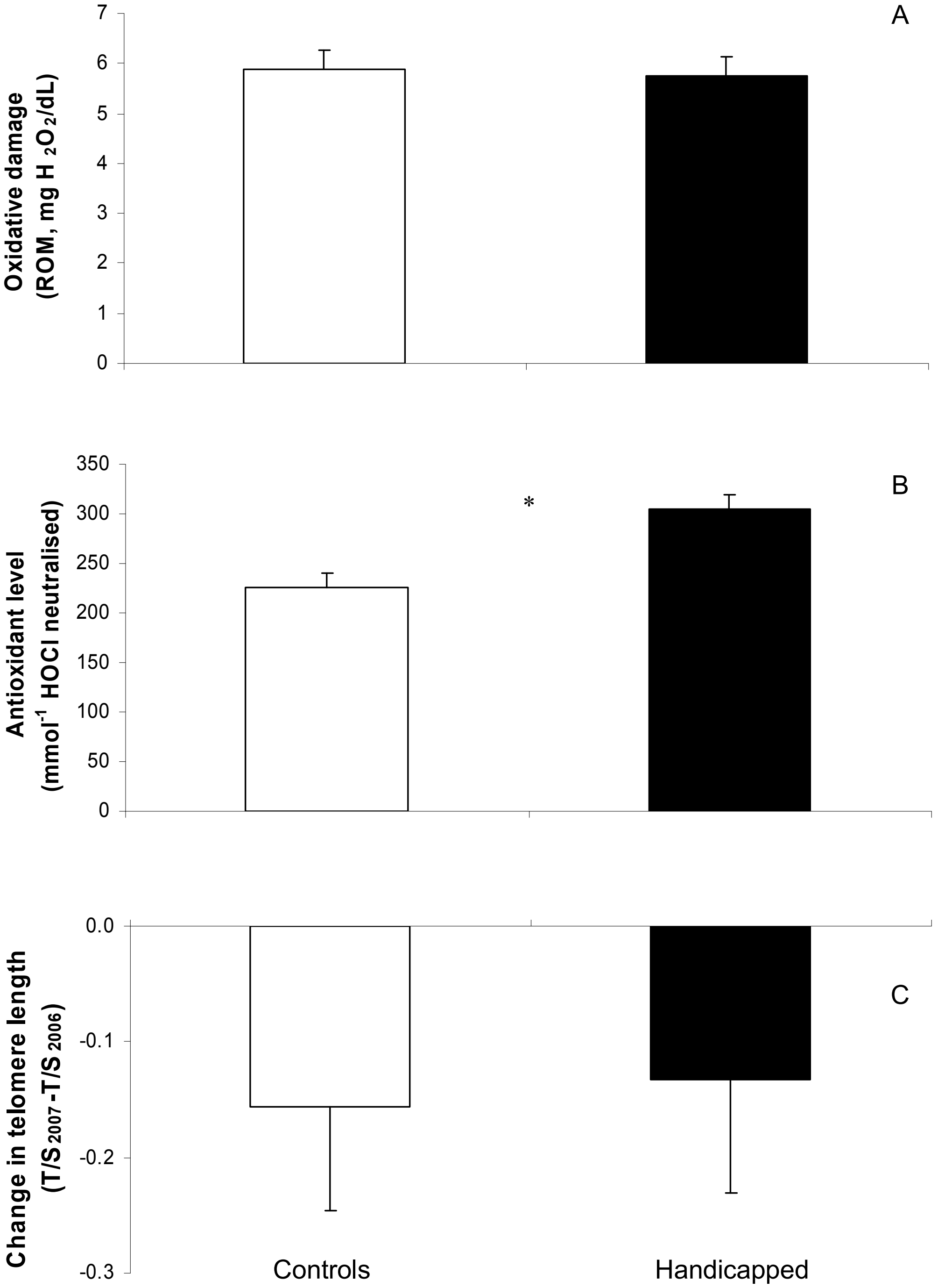

*Fig. 3: Oxidative damage (A) and antioxidant level (B) in 2006-07 and change in telomere length between 2006-07 and 2007-08 (C) in control Adélie penguins (white) and Adélie penguins handicapped during the breeding season in 2006-07 (black). * indicates a significant difference between control and handicapped penguins.*

Oxidative status, telomere shortening and fecundity

Clutch size was smaller in 2007-08 when females exhibited an increased antioxidant capacity one year before ($F_{1, 14}$= 5.22, P=0.04, Fig. 4). In contrast, clutch size in 2007-08 was not related to ROM levels in 2006-07 ($F_{1, 14}$= 0.83, P=0.38) or telomere shortening between the two years ($F_{1, 14}$= 2.69, P=0.13).

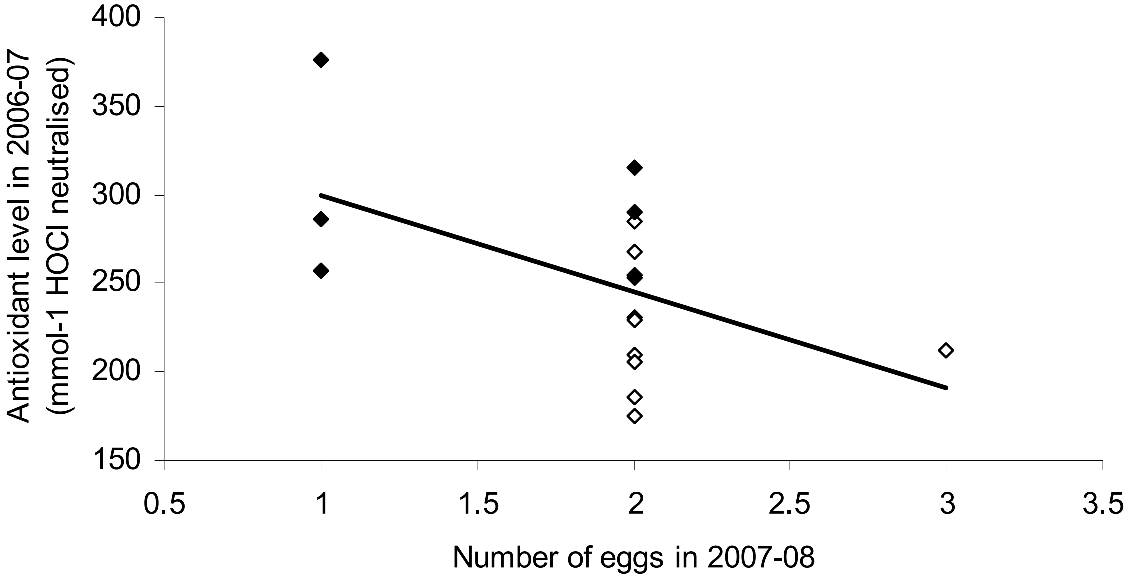

Fig. 4: Relationship between antioxidant levels in 2006-07 and clutch size in 2007-08 in control (white symbols) and handicapped females (black symbols).

DISCUSSION

The present study is the first to characterize the oxidative stress / telomere couple as a proximal mechanism explaining how long-lived species could counteract the negative impact of increased reproduction demands on self-maintenance. As expected in long-lived species, handicapped penguins subjected to increased breeding constraints appear to have solved the conflicting allocation of resources between reproduction and self-maintenance by giving priority to their own maintenance. Indeed, our longitudinal study showed that these birds increased their antioxidant capacity while oxidative damage and telomere shortening remained unchanged. In contrast, in the short-lived zebra finch, antioxidant defences decline with increased reproductive effort (Alonso-Alvarez et al. 2004, Wiersma et al. 2004). This discrepancy between oxidative status relative to breeding effort in the zebra finch and in the Adélie penguin is in agreement with life-history theory predicting that short-lived organisms are expected to give a lower priority to self-maintenance than long-lived animals when breeding constraints increase.

Cost of reproduction, mainly due to the alteration of adult body condition, has been previously noted in long-lived seabirds such as the kittiwakes (Golet et al. 1998, Jacobsen et al. 1995). In a more recent long-term study, the importance of adult body condition as an important mechanism has been however challenged, and other parameters such as physiological stress factors have been suggested to be more important (Golet et al. 2004). The idea that oxidative stress induces adverse effects on fecundity has been previously proposed (Beckman & Ames 1998, Barja 2004) and received recent support in another long-lived bird, the Alpine swift (Bize et al. 2008). In the latter study, females with the higher oxidative resistance were also those having the higher egg-laying capacity and beneficing from a higher hatching success. Therefore, immediate antioxidant capacity insures a good reproductive success (Blount et al. 2004, Bize et al. 2008). However, an unusual investment in self-maintenance is also correlated with a long-term reduction of female's reproductive output. This is illustrated by the fact that female Adélie penguins with high antioxidant levels in 2006-07 also suffered from a reduced fecundity the subsequent year (Fig. 4). Antioxidant mechanisms presumably require energy allocation and therefore may compete in the long term with the ability of females to recover from previous reproductive investment. In long-lived species, females are known to alternate reproductive seasons with high, low and non-investment in reproduction (Yoccoz et al. 2002). Yet, the exact mechanisms explaining the delayed negative impact of increased investment in antioxidant defenses on female fertility are unknown, but our results confirm that balancing antioxidant capability with other function is a part of the mechanisms that shape life-history trade-offs (Monaghan et al. 2008).

Oxidative stress has adverse effects on female fertility but has also been associated to reduced survival rates of males in Alpine swift (Bize et al. 2008). Indeed, oxidative stress is a corner stone mechanism to explain how ageing occurs (Beckman & Ames 1998) and some data provided a linked between oxidative damages and functional senescence of the organism (reviewed in Martin & Grotewiel 2006). However, since our longitudinal procedure was carried out on penguins that bred in two consecutive years, we cannot conclude on the link between oxidative stress and survival. In this line of thought, it would worthwhile examining whether investment in oxidative defense was done at the expense of future return rates.

In addition, we found that telomeres were longer in males than in females. This is in agreement with the higher inter-annual survival observed in males (Ainley & DeMaster 1980, Dugger et al. 2006), Interestingly, there was no difference in telomere shortening between sexes suggesting that female Adélie penguins had shorter telomeres at hatching or that telomere shortening was more important in females during the early stages of life. Concerning the experimental procedure, the additional breeding workload did not have any impact on telomere dynamics since the change of telomere length was similar in control and handicapped penguins. Three non-exclusive reasons are conceivable: (1) deleterious impacts on telomere length due to the handicap procedure will appear after a time longer than one year (indeed, the relationship between telomere size and survival rates appears significant only after 3-4 years in alpine swift (Bize et al. 2009), a bird with a comparable longevity); (2) DNA repair mechanisms such as telomerase were activated, then leading to telomere size maintenance (Monaghan & Hausmann 2006, Vleck et al. 2007); (3) handicapped penguins were able to increase their antioxidant barrier and did then protect their DNA from extra-damage due to ROS attack. Moreover, because the measurement of telomere dynamics necessarily implies the presence of breeding birds in two consecutive years, our results only apply to birds who returned to the colony the second year. Such a procedure may have resulted in the selection of the most competitive birds and may hide an immediate relationship between telomere size or loss and survival in our model, as expected from recent data showing that individuals with a slower telomere shortening were more likely to survive to the next year (Bize et al. 2009, Salomons et al. 2009).

Overall our results show that Adélie penguins ultimately preserve telomere size when faced with increased breeding constraint. They achieve this goal probably *via* a higher antioxidant protection, to buffer the inevitable rise in ROS production that follows changes in metabolic or in activity rates. Assuming that telomere dynamics predicts life expectancy in Adélie penguins, our experimental procedure is likely to have no long-term consequences for birds who returned to the colony to breed one year after the experiment. However, the higher priority given to self-maintenance had long-term costs since it altered the fecundity of females one year after the experiment. One important challenge in the future will be to determine the nature of the antioxidant processes involved, and to ultimately understand how the higher investment in antioxidant protection (and not oxidative stress) may alter fecundity and survival.

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Article 8 : Stress oxydant et stratégies de recherche alimentaire

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FORAGING IN AN OXIDATIVE ENVIRONMENT: RELATIONSHIP BETWEEN δ^{13}C VALUES AND OXIDATIVE STATUS IN ADELIE PENGUINS

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Foraging in an oxidative environment: relationship between δ^{13}C values and oxidative status in Adélie penguins

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The alternation of short/coastal and long/pelagic foraging trips has been proposed as a strategy for seabirds to reconcile self-feeding and parental care. Both types of foraging trips may result in different foraging efforts and diet qualities, and consequently are likely to modify the oxidative status of seabirds.

We examined the relationship between the oxidative status of Adélie penguins and (i) the duration of their foraging trips and (ii) their plasma δ^{13}C values reflecting their spatial distribution.

The oxidative status did not correlate with the foraging trip duration but with the δ^{13}C values: high values being associated with high levels of oxidative damage.

This relationship is likely to be related to the prey properties of penguins as both parameters are largely determined by the diet. Two non-exclusive hypotheses can be proposed to explain this relationship: (i) penguins foraging in coastal areas feed on a diet enriched in ^{13}C and depleted in antioxidant compounds; (ii) birds with low antioxidant capacity are constrained to forage in coastal areas.

Our study is the first to show that the adoption of different foraging strategies is associated with different levels of oxidative stress. However, further studies are needed to investigate the underlying mechanisms of this intriguing relationship.

Keywords: foraging; stable isotope; oxidative stress; seabirds

1. INTRODUCTION

One strategy adopted by seabirds to reconcile self-feeding and parental care consists in performing foraging trips of different durations. Short foraging trips result in increased provisioning rate to offspring while long foraging trips result in decreased provisioning rate but allow parents to restore their body reserves (Chaurand & Weimerskirch 1994; Weimerskirch 1995). The most plausible reason for why foraging trips are short or long is that seabirds adopt different spatial foraging distributions at sea: short trips are more coastal while long trips are more oceanic (Weimerskirch *et al.* 1997, 1998; Catard *et al.* 2000; Hamer *et al.* 2001).

This alternation in spatial foraging distribution may be associated with a change in the diet of seabirds (Weimerskirch *et al.* 1998; Cherel *et al.* 2005*a*). For instance, white-chinned petrels *Procellaria aequinoctialis* feed mainly on fish during short/coastal trips while they feed on krill and fish during long/pelagic trips (Catard *et al.* 2000). The biochemical composition of these prey items may differ and thereby influence the biochemistry and the physiology of the consumer. For example, two of the most common prey in the Austral Ocean, Antarctic krill *Euphausia superba* and fish, exhibit close energy and protein contents but differ both quantitatively and qualitatively in their fat and antioxidant contents. Krill contains less fat than fish (Yanagimoto *et al.* 1979; Friedrich & Hagen 1994) but more polyunsaturated fatty acids (Tierney *et al.* 2008) and antioxidants (Tou *et al.* 2007). As the antioxidant capacity of birds reflects the antioxidant content of their diet (as shown by the positive relationship between dietary antioxidants and blood antioxidant capacity in birds; Cohen *et al.* 2009), it is likely that seabirds feeding predominantly on krill exhibit higher antioxidant capacity than those feeding on fish. The selection of krill during long/pelagic trips, as observed in white-chinned petrels (Catard *et al.* 2000), may consequently be associated with a low oxidative stress, i.e. a high antioxidant capacity relative to the production of reactive oxygen species (ROS) (Finkel & Holbrook 2000). In contrast, because polyunsaturated fatty acids are more susceptible to peroxidation than monounsaturated fatty acids (Hulbert 2008), a diet with a high content of polyunsaturated fatty acids such as krill may be associated with higher oxidative stress (Jenkinson *et al.* 1999). Therefore, by selecting prey with different compositions during short/coastal and long/pelagic trips, seabirds may modulate their oxidative status, depending on the antioxidant content of their prey relative to the pro-oxidant effect of this prey (for instance, through its content in polyunsaturated fatty acids).

Moreover, the cost associated with the different foraging trips may also impact the oxidative status of seabirds. Indeed, short trips, energetically more costly than long trips (Weimerskirch *et al.* 2003), are likely to be related to higher oxygen consumption and consequently to greater ROS production (Loft *et al.* 1994).

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In the present study, we examined whether the oxidative status of Adélie penguins *Pygoscelis adeliae* was related to (i) the duration of their foraging trips and (ii) their plasma ratio $^{13}C/^{12}C$ (further referred to as $\delta^{13}C$) giving an index of the spatial distribution of birds (Kelly 2000; Inger & Bearhop 2008).

2. MATERIAL AND METHODS

We first examined the relationship between oxidative status and foraging strategies in penguins subject to the same environmental conditions but performing foraging trips of different durations. We took into consideration potential confounding factors susceptible to modulate foraging efforts such as the brood size, the sex of the parent and the sex of the chicks (Beaulieu *et al.* 2009). Then, we examined the relationship between oxidative status and foraging strategies for 2 years by considering when the same individuals changed the duration of their foraging trips as well as their spatial distribution because of different environmental conditions (Beaulieu *et al.* in press).

(a) *Study species*

The Adélie penguin is a long-lived species (maximum lifespan: 20 years; Ainley 2002) where breeding cycle comprises four phases: (i) the courtship from mid-October to early November; (ii) the incubation of one or two eggs for 30–36 days; (iii) the guard stage (from mid-December to mid-January) when both parents alternate foraging at sea and chick attendance at nest; and (iv) the crèche stage (from mid-January to mid-February) when both parents can forage at the same time leaving the chick(s) alone in the colony.

(b) *Fieldwork*

The study took place in Dumont d'Urville (66°40′S; 140°01′E), Adélie Land, Antarctica, in summers of 2006–2007 and 2007–2008. In 2006–2007, penguins performed short foraging trips and fed in more coastal areas than in 2007–2008 (Beaulieu *et al.* in press).

Eleven stable pairs were followed during the two consecutive summers. These pairs were visually identified during the courtship period and their nests were observed every 2 h to obtain the duration of their foraging trips throughout the breeding cycle (Beaulieu *et al.* in press). Penguins were weighed during the chick-rearing period, 40–45 days after egg-laying, when parents alternate periods at sea (duration: 1–2 days) and periods on the nest. At the same time, approximately 1.5 ml of blood was collected in heparinized syringes in less than 5 min after capture. Blood samples were then centrifuged and plasma samples were frozen at −20°C for further analyses.

In 2007–2008, among the 11 pairs, we selected those that had only one chick during the chick-rearing period. We completed this group with new pairs also with only one chick to avoid the potential bias owing to different brood size on foraging effort (Beaulieu *et al.* 2009). A sample of 18 pairs with one chick was then constituted and underwent the same procedure as that described above.

Adults were sexed by cloacal inspection and by observation of copulations. As foraging effort may be modulated by the sex of the chick, we also determined the sex of the chicks of the pairs monitored in 2007–2008, by molecular sexing from feathers collected at the end of the season (Beaulieu *et al.* 2009).

(c) *Laboratory analyses*

As previously described in birds (e.g. Costantini 2008; Costantini *et al.* 2007), oxidative stress was measured in plasma samples by using the d-reactive oxygen metabolites (d-ROM) and the oxy-adsorbent tests (Diacron International).

The d-ROM test measures plasmatic hydroperoxydes, a reactive oxygen metabolite (ROM) resulting from the attack of ROS on organic substrates (carbohydrates, lipids, amino acids, proteins, nucleotides). The plasma (4 μl) was first diluted in 200 μl of an acidic buffer solution (pH = 4.8) and 2 μl of chromogen (*N,N*-diethyl-*p*-phenylenediamine) and then incubated at 37°C for 75 min. These acidic conditions favour the release of iron ions from plasma proteins, which catalyse the breakdown of hydroperoxyde into alkoxyl and peroxyl radicals. These final products in turn react with the chromogen and produce a complex where colour intensity, read with a microplate reader (490 nm, Statfax3200, Awareness Technology Inc.), is proportional to its concentration. The concentration of hydroperoxyde was then calculated by comparison with a standard solution whose oxidative activity on the chromogen is equivalent to the activity of H_2O_2 ($0.08\ \mathrm{mg\,dl^{-1}}$). Measurements were therefore expressed as $\mathrm{mg\,dl^{-1}}$ H_2O_2 equivalents. Intra- and inter-assay coefficients of variations were 8 per cent and 6 per cent, respectively.

The oxy-adsorbent test measures the total plasma antioxidant capacity. This test evaluates the plasma ability to oppose the massive oxidative action of a hypochlorous acid (HClO) solution. The plasma (2 μl) was first diluted 1 : 100 with distilled water; 5 μl of this solution was then incubated with 200 μl of a titred HClO solution at 37°C for 10 min. Then, 5 μl of chromogen (*N,N*-diethyl-*p*-phenylenediamine) was added to measure the excess of HClO in plasma. The resulting coloured complex, read with a spectrophotometer (490 nm, Statfax3200, Awareness Technology Inc.), is inversely related to the antioxidant power. The plasmatic antioxidant capacity was then calculated by comparison with a standard solution. Measurements were expressed as $\mathrm{mmol^{-1}}$ HOCL neutralized. Intra- and inter-assay coefficients of variations were 7 per cent and 4 per cent, respectively.

As phytoplankton, at the base of marine foodwebs, is richer in ^{13}C values in coastal than in pelagic areas (France 1995), animals foraging and feeding in coastal areas exhibit higher $\delta^{13}C$ values than pelagic foragers (Cherel & Hobson 2007). Moreover, isotopic values mirror the diet throughout the period of tissue synthesis (Kelly 2000; Inger & Bearhop 2008). Therefore, our ^{13}C measurements on plasma, whose turnover is about 3 days (Hobson & Clark 1993), reflected the diet of penguins during the foraging trip preceding blood sample. Isotopic analyses were carried out at the Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA, France). As recommended by Cherel *et al.* (2005*b*), plasma samples (200 μl) were delipidated, as lipids, depleted in ^{13}C, decrease plasmatic $\delta^{13}C$ values (Cherel *et al.* 2005*a*). Then, they were lyophilized (48 h) and powdered (Hobson *et al.* 1997). Results are expressed in the standard δ notation (‰) relative to PDB (PeeDee Belemnite). Intra- and inter-assay coefficients of variation were 0.88 per cent and 0.42 per cent, respectively. This technique has already allowed us to highlight different spatial distributions of Adélie penguins according to sea-ice conditions: in 2007–2008, when fast ice remains for longer in Adélie Land than in 2006–2007, penguins foraged in more oceanic areas (Beaulieu *et al.* in press).

(d) *Statistical analyses*

First, we assessed in 2007–2008 whether body mass, $\delta^{13}C$ values, oxidative status and the duration of the foraging trip preceding blood sampling differed between males and females. As the sex of the chick affects foraging trip duration (Beaulieu *et al.* 2009), we also considered this parameter and we used general linear models (GLMs) with the sex of the adult, the sex of the young and their interaction as fixed factors. For the duration of foraging trips, data were log-transformed to obtain normality of residuals. Second, we conducted Pearson or Spearman correlations (according to normality of data) to investigate the relationships between parameters in males and females. When the GLMs indicated no differences between sexes, we conducted the same correlations including males and females together. Inter-annual comparison for oxidative status was carried out by using general linear mixed models (GLMMs) to avoid the problem of pseudoreplication as our statistical analyses involved the same penguins. Individuals were considered as a random factor while the year, the sex and their interaction were used as fixed factors. Normality of residuals was assessed with a Shapiro–Wilk test.

All analyses were conducted using SPSS 16.02 (SPSS Inc.). Results are expressed as means ± s.e. and significance level was set at $\alpha = 0.05$.

3. RESULTS

(a) *Intra-annual analyses (2007–2008)*

Males were heavier than females when blood was sampled (5.16 ± 0.11 and 4.46 ± 0.11 kg, respectively) and they had performed shorter foraging trips than females (1.10 ± 0.15 and 1.74 ± 0.15 days, respectively) before blood sampling (table 1). Neither the adult sex nor the chick sex affected $\delta^{13}C$ values or the oxidative status of parents (table 1): $\delta^{13}C$ values (-25.74 ± 0.12 and -25.63 ± 0.12‰, respectively), ROM levels (6.64 ± 0.52 and $6.90 \pm 0.51\ \mathrm{mg\ H_2O_2\ dl^{-1}}$, respectively) and the antioxidant capacity (185.37 ± 18.56 and $171.13 \pm 18.28\ \mathrm{mmol^{-1}}$ HOCL neutralized, respectively) were similar in males and females.

As $\delta^{13}C$ and oxidative values were independent of adult sex, data of male and female were first pooled. ROM levels were positively correlated with $\delta^{13}C$ values and negatively correlated with the antioxidant capacity of birds (figure 1). These trends were found in males and females although they were not significant for females (figure 2). In contrast, body mass and foraging trip duration before blood sampling were not correlated with $\delta^{13}C$ values or the oxidative status (all $p > 0.05$).

Within pairs, the males' and females' body mass were not related (Pearson correlation: $r = 0.034$, $p = 0.896$). In contrast, there was a significant positive relationship between males' and females' $\delta^{13}C$ values and between males' and females' oxidative status (figure 2).

(b) *Inter-annual analyses (2006–2007 versus 2007–2008)*

The sex of penguins had no effect on ROM levels (GLMM: $F_{1,18} = 1.42$, $p = 0.25$) and on their antioxidant capacity (GLMM: $F_{1,18} = 1.06$, $p = 0.32$). However, there was a strong inter-annual effect (figure 3): in 2006–2007, when penguins foraged in more coastal areas, ROM levels were higher (GLMM: $F_{1,18} = 27.00$, $p < 0.001$) and their antioxidant capacity was lower (GLMM: $F_{1,18} = 27.03$, $p < 0.001$) than in 2007–2008 when sea-ice conditions forced the penguins to forage in more oceanic areas (Beaulieu *et al.* in press).

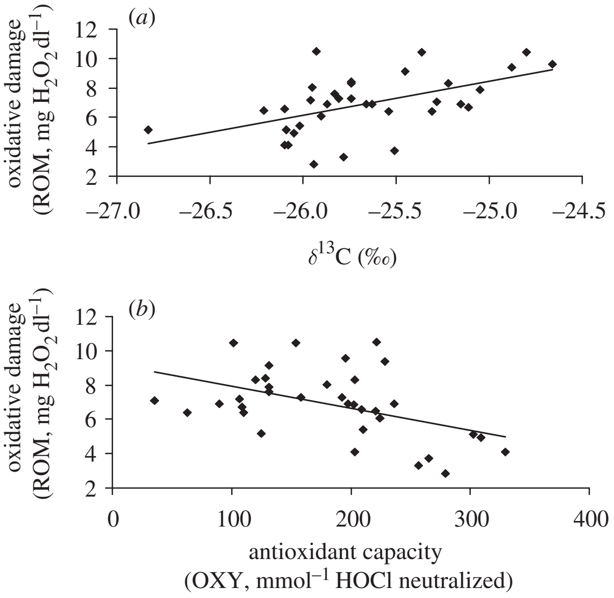

Figure 1. Scatter plots showing the relationships between (*a*) $\delta^{13}C$ values and oxidative damage: $r = 0.531$; $p = 0.001$. (*b*) Oxidative damage and antioxidant capacity: $r = -0.463$; $p = 0.005$.

Table 1. Results of general linear models (GLMs) assessing the influence of the sex of the adult and the chick on adult body mass, $\delta^{13}C$ ratio, oxidative status and the duration of the foraging trip preceding blood sampling.

	adult sex		chick sex		interaction	
	F	*p*	*F*	*p*	*F*	*p*
body mass	13.342	0.001	1.527	0.226	1.301	0.263
$\delta^{13}C$	0.416	0.524	0.251	0.620	0.010	0.920
ROM	0.122	0.730	1.483	0.232	0.170	0.683
OXY	0.299	0.589	0.873	0.357	0.180	0.674
foraging trip duration	11.446	0.002	2.217	0.147	0.287	0.596

4. DISCUSSION

Foraging trip duration has been found to be related to energy expenditure with short foraging trips being more costly than long foraging trips (Weimerskirch *et al.* 2003). As high energy expenditure is likely to increase oxidative stress through increased oxygen consumption (Loft *et al.* 1994), we expected foraging trip duration and oxidative status also to be related. However, in our study, foraging trip duration was not related to the oxidative status of penguins.

Instead of a relationship between the oxidative status and the foraging trip duration, we found a relationship

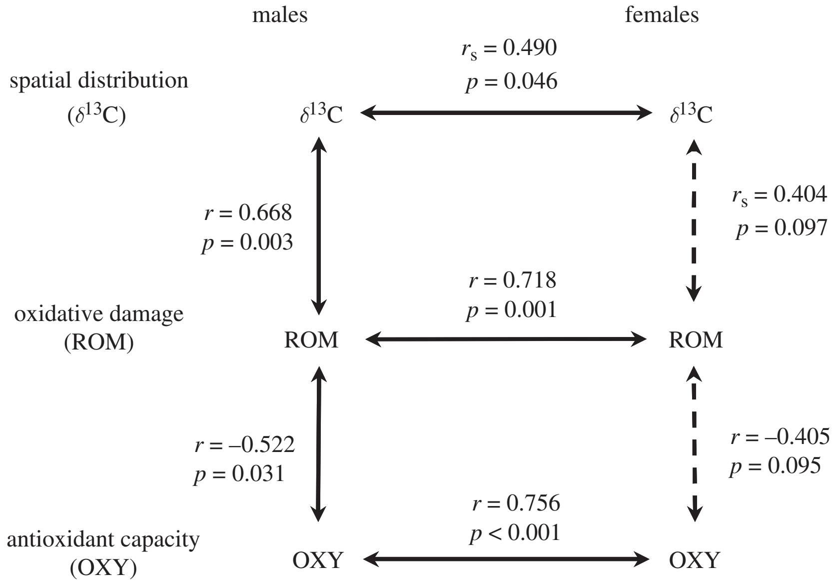

Figure 2. Relationships between the spatial distribution and the oxidative status in male and female Adélie penguins and between males and females within pairs. Solid arrows: significant relationships; dashed arrows: non-significant relationships.

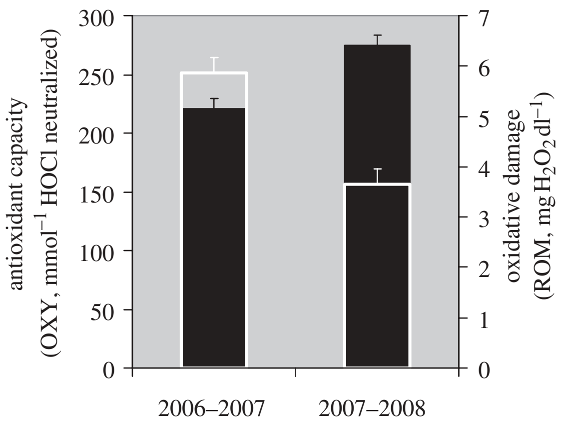

Figure 3. Oxidative damage (white histograms) and antioxidant capacity (black histograms) in the same group of 11 stable pairs of Adélie penguins in 2006–2007 and 2007–2008.

between the oxidative status and δ^{13}C values of penguins: penguins with higher plasmatic δ^{13}C values also experience greater oxidative damage. To our knowledge, no other study has previously described this relationship at the scale of the organism. As δ^{13}C values and the antioxidant capacity of birds are largely determined by food intake (Inger & Bearhop 2008; Cohen *et al.* 2009), differences in diet quality can be implicated.

Firstly, a direct impact of food ^{13}C content on the likelihood to suffer from more oxidative stress can be suggested. It has been proposed that a diet enriched in ^{13}C might decrease damage caused by ROS on proteins, nucleic acids or lipids, as biomolecules that incorporate heavier isotopes such as ^{13}C may be more stable and successfully resist to oxidative stress (Shchepinov 2007). In disagreement with this hypothesis, Adélie penguins, feeding on a diet richer in ^{13}C than terrestrial birds (Inger & Bearhop 2008), exhibit higher ROM levels than most terrestrial bird species (reviewed in Costantini *et al.* 2007). Moreover, in our study, penguins with higher δ^{13}C values also had higher oxidative damage. This suggests that the potential beneficial direct effect of ^{13}C on oxidative status is negligible compared with other parameters such as the antioxidant properties of the diet (Cohen *et al.* 2009).

In Adélie Land, Adélie penguins rely mainly on Antarctic krill and Antarctic silverfish (*Pleuragramma antarcticum*, Ridoux & Offredo 1989). Antioxidant levels are higher in krill than in fish (Tou *et al.* 2007) and may explain the inter-annual differences in the antioxidant status of penguins observed in our study. Indeed, the contribution of fish, poorer in antioxidants, was slightly more important in the penguins' diet in 2006–2007 (Beaulieu *et al.* in press) when their antioxidant capacity was lower. In addition, Antarctic silverfish inhabit more coastal areas (with higher δ^{13}C values) than Antarctic krill (Cherel 2008). This suggests that the relationship between the δ^{13}C values and the oxidative status of penguins is likely to be due to the different antioxidant levels of their prey living predominantly either in coastal (fish) or in oceanic (krill) areas.

Krill also contains higher levels of polyunsaturated fatty acids than fish (Tierney *et al.* 2008), a class of lipids known to have a pro-oxidant impact at the cell (Mazière *et al.* 1999) and organism levels (Jenkinson *et al.* 1999). In humans, a diet enriched with 15 per cent of polyunsaturated fatty acids adversely affects lipid peroxidation levels. However, the coupling of antioxidant treatments to diets rich in polyunsaturated fatty acids has been suggested to re-equilibrate the oxidative balance (Jenkinson *et al.* 1999). This is likely to be the case in penguins, as krill, rich in polyunsaturated fatty acids, is also characterized by high antioxidant contents.

Another hypothesis explaining the relationship between oxidative status and δ^{13}C values of penguins (and therefore their foraging distribution) could be that birds with high antioxidant capacity and thus low oxidative damage were able to forage in oceanic waters while those with low antioxidant capacity and high oxidative damage were constrained to forage in coastal waters. In birds, age affects the antioxidant capacity (Bize *et al.* 2008; Costantini 2008), the foraging effort and the spatial foraging range of seabirds (Catry *et al.* 2006) that, in turn, may also affect oxidative status. As there is an assortative mating by age in Adélie penguins (Reid 1988), this may explain the positive correlation between males' and females' oxidative statuses and between males' and females' δ^{13}C values. This suggests that male and female Adélie penguins of similar age and oxidative status share the same foraging spatial distribution.

In conclusion, our study revealed that, in contrast to foraging trip duration, the oxidative status of Adélie penguins was related to δ^{13}C ratios and therefore presumably to the spatial distribution of their prey. To go further into the understanding of the respective influences of diet and age on the oxidative status of penguins, an experimental approach appears necessary. In this context, it would be worthwhile to measure the oxidative status of penguins in captivity fed with different controlled diets (e.g. krill versus fish), in parallel with a longitudinal study examining the changes in oxidative status of known-age penguins over their lifetime.

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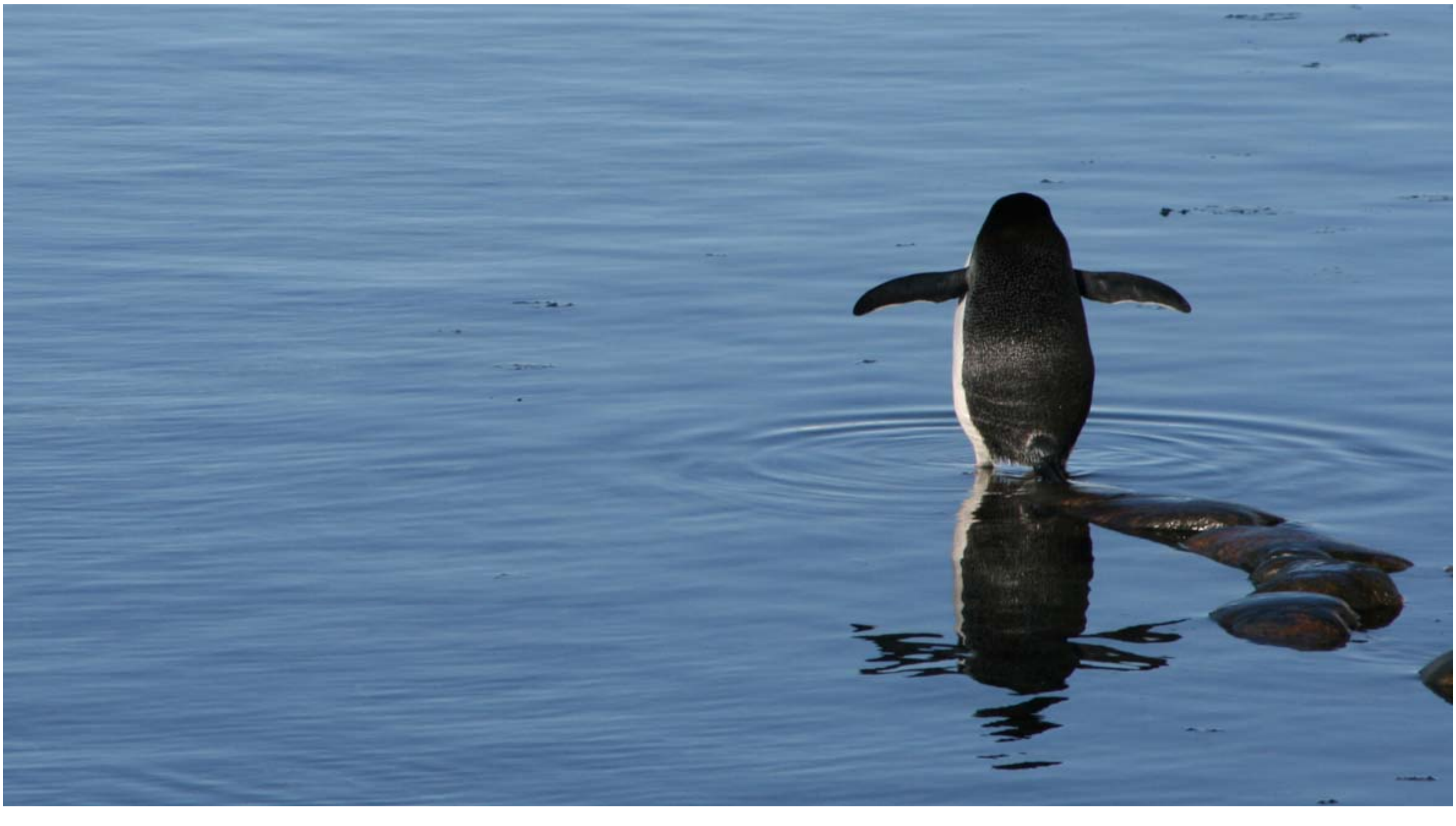
4

SYNTHESE,
DISCUSSION & PERSPECTIVES



Synthèse, Discussion & Perspectives

Dans cette partie, les résultats concernant les deux contraintes sont discutés et mis en relation avec les données de la littérature disponibles principalement chez les espèces longévives. Il y est tout d'abord question de la réponse comportementale des individus face à la contrainte, puis de la réponse de leurs partenaires et des conséquences pour leur progéniture. Les changements hormonaux et les modifications des niveaux des métabolites et du statut oxydant sont ensuite abordés. Enfin, dans une dernière partie, nous nous intéressons aux conséquences à long terme.

Les discussions sont par ailleurs détaillées dans chacun des articles joints à ce manuscrit.

L'ensemble des résultats est résumé dans le Tableau 2 pour la contrainte expérimentale et dans le Tableau 3 pour la contrainte environnementale.

Tableau 2 : Récapitulatif des résultats principaux obtenus pour la contrainte expérimentale. Case jaune : modification de paramètre (+ : augmentation, − : diminution), case grise (=) : aucune modification par rapport aux manchots contrôles, case blanche (NE) : paramètre non étudié.

<table>
<tr><td colspan="5" rowspan="2"></td><td colspan="2">Couples "mâles handicapés"</td><td colspan="2">Couples "femelles handicapées"</td></tr>
<tr><td>Mâles handicapés</td><td>Femelles partenaires</td><td>Femelles handicapées</td><td>Mâles partenaires</td></tr>
<tr><td rowspan="18">Année N</td><td rowspan="15">Adultes</td><td rowspan="4">Mer</td><td rowspan="2">Voyage alimentaire</td><td>Durée</td><td>+</td><td>=</td><td>+</td><td>=</td></tr>
<tr><td>Distribution spatiale</td><td colspan="4">Plus côtier</td></tr>
<tr><td rowspan="2">Plongée</td><td>Temps au fond</td><td>+</td><td>NE</td><td>NE</td><td>NE</td></tr>
<tr><td>Temps entre 2 plongées</td><td>+</td><td>NE</td><td>NE</td><td>NE</td></tr>
<tr><td rowspan="14">Terre</td><td rowspan="2">Incubation</td><td>Température</td><td>=</td><td>NE</td><td>NE</td><td>NE</td></tr>
<tr><td>Taux de rotation</td><td>+</td><td>NE</td><td>NE</td><td>NE</td></tr>
<tr><td colspan="2">Masse corporelle</td><td>−</td><td>=</td><td>−</td><td>=</td></tr>
<tr><td colspan="2">Nourrissage des poussins</td><td colspan="4">=</td></tr>
<tr><td colspan="2">Niveau trophique</td><td colspan="4">=</td></tr>
<tr><td rowspan="6">Physiologie</td><td>Corticostérone</td><td colspan="4">=</td></tr>
<tr><td>Prolactine</td><td colspan="2">=</td><td>−</td><td>=</td></tr>
<tr><td>Acide urique</td><td colspan="4">=</td></tr>
<tr><td>Triglycérides</td><td colspan="4">=</td></tr>
<tr><td>Dommages oxydatifs</td><td>=</td><td>NE</td><td>=</td><td>NE</td></tr>
<tr><td>Capacité antioxydante</td><td>+</td><td>NE</td><td>+</td><td>NE</td></tr>
<tr><td rowspan="3">Poussins</td><td colspan="2">Nombre</td><td colspan="2">−</td><td colspan="2">=</td></tr>
<tr><td colspan="2">Masse corporelle</td><td colspan="4">−</td></tr>
<tr><td colspan="2">Sollicitations</td><td colspan="4">=</td></tr>
<tr><td rowspan="4">Année N+1</td><td rowspan="4">Adultes</td><td rowspan="4">Terre</td><td colspan="2">Taux de retour</td><td>−</td><td colspan="3">=</td></tr>
<tr><td colspan="2">Stabilité des couples</td><td colspan="2">−</td><td colspan="2">=</td></tr>
<tr><td colspan="2">Fécondité</td><td>NE</td><td>=</td><td>−</td><td>NE</td></tr>
<tr><td colspan="2">Raccourcissement des télomères</td><td>=</td><td>NE</td><td>=</td><td>NE</td></tr>
</table>

Tableau 3 : Récapitulatif des résultats principaux obtenus pour la contrainte environnementale. Case jaune : modification de paramètre (+ : augmentation, − : diminution), case grise (=) : aucune modification, case blanche (NE) : paramètre non étudié. L'année de référence (2006-07) est l'année où l'étendue de glace était moins importante (par exemple, "+" signifie que le paramètre était augmenté en 2007-08 par rapport à 2006-07).

					Mâles	Femelles
Année N	Adultes	Mer	Voyage alimentaire	Durée	+	
				Distribution spatiale	Plus océanique	
			Plongée	Temps au fond	−	NE
				Temps entre 2 plongées	−	NE
		Terre	Incubation	Température	NE	
				Taux de rotation	NE	
			Masse corporelle		=	
			Nourrissage des poussins		NE	
			Niveau trophique		−	
			Physiologie	Corticostérone	=	
				Prolactine	−	
				Acide urique	+	
				Triglycérides	+	
				Dommages oxydatifs	−	
				Capacité antioxydante	+	
	Poussins		Nombre		=	
			Masse corporelle		=	
			Sollicitations		NE	
Année N+1	Adultes	Terre	Taux de retour*		=	
			Stabilité des couples*		=	
			Fécondité		NE	
			Raccourcissement des télomères		NE	

*Ces résultats n'apparaissent pas dans les articles présentés ci-dessus

I – Réponse comportementale face aux deux contraintes

I.1 – Résultats de cette étude

La conséquence la plus visible des deux contraintes de reproduction envisagées dans ce mémoire est la modulation de la durée des voyages alimentaires : 70% plus longs chez les individus handicapés (Article 1), cette tendance s'inversant lorsque la glace de mer disparaît tôt dans l'année (20% plus courts en 2006-07 ; Article 3). Ainsi en considérant la durée des voyages alimentaires, l'année où la glace s'est retirée plus tardivement apparaît comme la plus contraignante pour les manchots. Comme d'autres études l'ont déjà montré chez le manchot Adélie (Watanuki *et al.* 1993, Nicol *et al.* 2008), cette différence dans la durée des voyages alimentaires reflète très probablement une différence de disponibilité alimentaire ; l'accessibilité aux proies des manchots handicapés étant très certainement réduite, de même que lorsque la glace de mer a persisté plus longtemps. Dans le cas de la contrainte environnementale, les manchots continuaient à effectuer des voyages plus longs même lorsque la glace de mer avait finalement disparu (Article 3), ce qui suggère que la persistance de la glace n'a pas uniquement agi comme une barrière physique entre les manchots et leurs espèces proies mais aussi qu'elle a rendu ces espèces proies moins disponibles *a posteriori*.

L'augmentation de la durée des voyages alimentaires associée à la contrainte expérimentale étant bien plus importante que celle associée à la contrainte environnementale, la procédure expérimentale a certainement conduit à une diminution de l'accessibilité aux proies plus marquée que la contrainte environnementale. Néanmoins, les manchots ont adapté leur comportement de plongée de manière similaire en modulant le temps passé au fond à la recherche de nourriture (Article 4). Ces différences de comportement de plongée peuvent également être mises en relation avec un changement partiel de la qualité des proies dans le régime des manchots, comme le laissent à penser les valeurs $\delta^{15}N$ légèrement (mais significativement) plus élevées l'année où le temps passé au fond était plus long. Comme déjà montré chez le manchot papou (*Pygoscelis papua* ; Lescroël *et al.* 2005), cela suggère qu'une légère augmentation de la contribution en poisson (relativement au krill) dans le régime des manchots (Article 6) s'accompagne d'un temps passé au fond à la recherche de nourriture plus long (Article 4).

Enfin, les manchots ont également modulé leur distribution spatiale face aux deux contraintes : la persistance de la glace de mer (dans les zones côtières) les a contraint à prospecter dans des zones plus océaniques (Article 6) alors que les manchots handicapés se sont alimentés dans des zones plus côtières (Article 5). Ce changement de stratégie de la part des manchots handicapés leur a certainement permis de minimiser le surcoût énergétique lié au handicap (Culik & Wilson 1991) en diminuant les phases de transit entre la colonie et les zones de pêche et ainsi de rentabiliser le temps passé à se nourrir.

I.2 – Comparaison aux données de la littérature

Concernant la procédure expérimentale, notre étude se trouve à cheval sur deux thématiques : d'une part, l'étude des effets de l'équipement chez le manchot Adélie (Tableau 1) et l'étude de l'investissement parental chez des oiseaux longévifs handicapés (Tableau 4). Bien évidemment, ces deux thématiques se recoupent mais l'approche est différente : dans un cas, les effets négatifs sont à éviter, dans l'autre cas, ils sont voulus.

L'augmentation de la durée des voyages alimentaires et la perte de masse des manchots handicapés sont en parfaite adéquation avec les résultats des études ayant utilisé des enregistreurs dont la taille était proche de celle de nos handicaps (Tableau 1).

Dans le cas des études ayant eu pour but de moduler le comportement parental en handicapant un des deux membres du couple, toutes ont recherché si l'individu handicapé présentait une masse corporelle diminuée (Tableau 4). Les résultats ne montrent pas de tendance générale ; certains individus présentant une masse diminuée, d'autres réussissant à la maintenir constante. Cette différence est très certainement due à des niveaux de contraintes et de disponibilité alimentaire différents entre les études. Cependant, cela peut également s'expliquer par le fait que les parents handicapés ne perdant pas de masse sont également ceux qui ont diminué la quantité de nourriture accordée à leurs poussins (Wanless *et al.* 1988, Sæther *et al.* 1993, Weimerskirch *et al.* 1999) alors que ceux dont la masse corporelle a diminué, ont maintenu une quantité de nourriture constante pour leurs poussins à chaque retour au nid (Article 1).

L'augmentation de la durée des voyages alimentaires représente la seule tendance commune à toutes les études : la durée des voyages alimentaires apparaît donc comme le paramètre le plus sensible au handicap (et donc à la disponibilité alimentaire) puisqu'elle est modifiée quel que soit le niveau de contrainte exercé. A l'inverse, très peu d'études ont essayé de relier l'augmentation de la durée des voyages alimentaires à des changements de comportement alimentaire : seuls Navarro & Gonzáles-Solís (2007) ont montré, comme dans notre étude, que les individus handicapés se distribuaient différemment sur les aires de recherche alimentaire mais gardaient le même régime alimentaire.

Tableau 4 : Récapitulatif des études ayant modulé l'effort parental chez des oiseaux longévifs en handicapant un des deux parents et ayant étudié les conséquences de cette contrainte sur le comportement de ce parent.

Etude	Wanless *et al.* 1988	Sæther *et al.* 1993	Tveraa *et al.* 1997	Weimerskirch *et al.* 1999	Duriez *et al.* 2000	Velando 2002	Velando & Alonso-Alvarez 2003	Paredes *et al.* 2005	Navarro & Gonzáles-Solís* 2007	Harding *et al.* 2009	Bijleveld & Mullers 2009	Article 1
Espèce	Guillemot de Troïl *Uria aalge*	Pétrel antarctique *Thalassoica antarctica*	Pétrel antarctique *Thalassoica antarctica*	Prion antarctique *Pachyptila desolata*	Prion de Belcher *Pachyptila belcheri*	Fou à pieds bleus *Sula nebouxii*	Fou à pieds bleus *Sula nebouxii*	Guillemot de Brünnich *Uria lomvia*	Puffin cendré *Calonectris diomedea*	Mergule nain *Alle alle*	Fou du Cap *Morus capensis*	Manchot Adélie *Pygoscelis adeliae*
Procédure expérimentale	Résistance hydrodynamique	Surpoids	Surpoids	Surpoids	Surpoids	Portance alaire diminuée	Portance alaire diminuée	Surpoids, Résistance hydrodynamique	Surpoids	Portance alaire diminuée	Portance alaire diminuée	Résistance hydrodynamique
Voyages alimentaires plus longs	Oui	Oui	Oui	Oui	Oui	-	-	Oui	Oui	-	Oui	Oui
Distribution spatiale différente	-	-	-	-	-	-	-	-	Oui	-	-	Oui
Paramètres de plongées modifiés	-	-	-	-	-	-	-	-	-	-	-	Oui
Changement de régime alimentaire	-	-	-	-	-	-	-	-	Non	-	-	Non
Perte de masse	Non	Non	Oui	Non	Non	Oui	Non	Oui	Non/Oui	Oui	Oui	Oui
Taille des repas diminuée	Oui	Oui	-	Oui	Non	-	-	-	-	-	-	Non

* complété par Navarro *et al.* 2008.

Tout comme les études faisant appel au handicap, l'ensemble des études traitant d'une contrainte environnementale chez le manchot Adélie confirme bien que le paramètre le plus sensible est la durée des voyages alimentaires ; celle-ci augmentant lorsque les conditions sont défavorables. Comparée aux autres études, l'augmentation de la durée des voyages alimentaires dans notre étude était relativement peu importante (Tableau 5), suggérant que la différence de disponibilité alimentaire entre 2006-07 et 2007-08 n'était pas trop sévère. Malgré cela, les manchots ont tout de même modifié leur comportement de plongée (en modulant le temps passé au fond) et leur régime alimentaire. Deux autres études ont examiné le comportement de plongée du manchot Adélie dans des conditions environnementales différentes (Watanuki *et al.* 1993, Rodary *et al.* 2000). Alors que nous avons trouvé que les manchots passaient plus de temps au fond quand la débâcle avait lieu plus tôt (Article 4), ces deux études ont montré que les manchots plongeaient plus profondément et plus longtemps quand le niveau de disponibilité alimentaire était diminué (Watanuki *et al.* 1993) ou en l'absence de glace de mer (Rodary *et al.* 2000). Cette même observation peut provenir de deux causes différentes : (1) lorsque la disponibilité alimentaire est faible, les manchots doivent augmenter leur effort de recherche alimentaire en prospectant plus longtemps et plus profondément (Watanuki *et al.* 1993) et (2) la présence de glace de mer empêche la lumière de pénétrer profondément dans l'eau, ce qui contraint les manchots à chercher leur nourriture plus près de la surface (Rodary *et al.* 2000). Les résultats obtenus dans notre étude (Article 4) ne peuvent être mis en relation avec ceux de Rodary *et al.* (2000) dans la mesure où le comportement de plongée a été étudié dans notre étude une fois que la glace de mer s'était retirée. Les différences observées entre les deux années considérées dans notre étude sont donc plus à rapprocher d'une différence de disponibilité alimentaire, tout comme dans l'étude de Watanuki *et al.* (1993). Cependant les auteurs de cette étude n'ont pas examiné le temps passé au fond à la recherche de nourriture. Or il est probable que, comme dans notre étude, celui-ci ait augmenté et pourrait expliquer pourquoi les plongées étaient plus longues. Comme le suggère l'augmentation de la durée des voyages alimentaires dans l'étude de Watanuki *et al.* (1993), il se peut que la différence de disponibilité alimentaire soit bien plus importante dans cette étude que dans la nôtre (Tableau 5). Ainsi, on peut imaginer que le temps passé au fond est le paramètre de plongée le plus sensible aux variations de disponibilité alimentaire alors que la durée et la profondeur de plongée ne sont modifiées que lorsque la disponibilité alimentaire est largement diminuée.

Par ailleurs, Watanuki *et al.* (1993) et Nicol *et al.* (2008) ont montré comme notre étude, que les manchots pouvaient se reporter vers d'autres espèces proies lorsque les conditions deviennent défavorables. En l'occurrence, les manchots Adélie se reportent vers la calandre antarctique *P. antarcticum* lorsque la disponibilité en krill diminue. Enfin, ce changement de régime alimentaire ne semble possible qu'à certains endroits et uniquement pendant certaines années (ex : études de Clarke *et al.* 2002 *vs.* Nicol *et al.* 2008 à Béchervaise Island). Cela suggère que les manchots sont capables d'ajuster leur comportement (plongées, régime...) si les conditions propres au milieu le leur imposent (ex : proies alternatives trouvées à des profondeurs différentes de celles de la proie habituelle) et surtout le leur permettent (ex : absence ou présence de proies alternatives).

Enfin, un autre levier sur lequel les manchots Adélie peuvent également jouer est la durée du stade de garde ; celle-ci étant plus longue lorsque les conditions environnementales sont moins favorables. Cela suggère que la croissance des poussins est plus lente lorsque les conditions sont défavorables et que les parents ne laissent leurs poussins seuls qu'au delà d'une certaine masse et/ou taille.

Tableau 5 : Récapitulatif des études ayant examiné la réponse comportementale du manchot Adélie dans des conditions environnementales différentes. Les études sont classées de gauche à droite en fonction de l'importance de l'augmentation de la durée des voyages alimentaires.

Etude	Clarke *et al.* 2002 [a]	Nicol *et al.* 2008	Olmastroni *et al.* 2004	Watanuki *et al.* 1993	Clarke *et al.* 2002 [b]	Articles 3 et 4
Localisation	Béchervaise Island	Béchervaise Island	Edmonson Point	Hukuro Cove	Béchervaise Island	Dumont d'Urville
Diminution de la masse en début de saison	Non	Non	Oui	Oui	Non	Non
Augmentation de la durée des voyages alimentaires	♀(30%) ♂ (20%)	♀ (50%) ♂ (40%)	-	70%	♀ (150%) ♂ (30%)	♀ (30%) ♂ (15%)
Distribution spatiale différente	-	Oui	-	-	-	Oui
Paramètres de plongée modifiés	-	-	-	Non	-	Oui
Changement de régime	Non	Oui	-	Oui	Non	Oui
Diminution de la quantité de nourriture dans l'estomac	Oui	Oui	-	Non	Oui	-
Augmentation de la durée du stade de garde	-	Oui	Oui	Oui	-	(Oui)

[a] Données de Clarke *et al.* (2002) pour les années 1997 et 1998
[b] Données de Clarke *et al.* (2002) pour les années 1993 et 1994

II – Réponse comportementale du partenaire face à la contrainte expérimentale

II.1 – Résultats de cette étude

Les résultats de notre étude n'ont pas permis de mettre en évidence de comportement de compensation de la part du partenaire envers les poussins lorsqu'un des deux parents était handicapé. Par ailleurs, du fait des voyages alimentaires 70% plus longs effectués par les manchots handicapés, les partenaires des manchots handicapés ont dû jeûner 70% plus longtemps que des manchots contrôles sur le nid. Or, ils n'ont pas perdu plus de masse[15] et la durée de leurs voyages alimentaires était comparable à celle des manchots contrôles (Article 1) suggérant que leur effort de pêche a dû être plus important que celui des contrôles. Cette hypothèse a été confortée par les teneurs de $\delta^{13}C$ mesurées dans leurs globules rouges. En effet, ces valeurs plus élevées chez les manchots partenaires que chez les manchots contrôles suggèrent que les partenaires se sont alimentés dans des zones plus côtières (Article 5), certainement de façon à minimiser le temps de transit au profit du temps de recherche alimentaire à proprement parler. Une étude plus approfondie de leur comportement de plongée à l'aide d'enregistreurs de plongées et de systèmes de localisation satellite (ex : GPS) suffisamment petits pour ne pas générer d'impact négatif, permettrait de confirmer si les manchots partenaires de manchots handicapés compensent la déficience de leur partenaire au moins pour eux-mêmes en changeant leur comportement de prospection alimentaire.

II.2 – Comparaison aux données de la littérature

L'étude du comportement du partenaire d'animaux désavantagés lors de la reproduction chez des espèces longévives semble être d'actualité puisque trois articles (sur un total de sept) traitant de ce sujet ont été publiés en 2009 (Tableau 6). Parmi ces sept publications, cinq présentent des paramètres suggérant qu'il y a compensation vis-à-vis de la déficience de

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[15] Si l'on considère que les manchots perdent 50 g par jour passé à jeûner (Chappell *et al.* 1993b), les partenaires des manchots handicapés auraient dû théoriquement peser ~250 g de moins que les manchots contrôles au moment de la deuxième pesée. Par ailleurs, si l'on considère que l'accumulation d'un gramme de protéine ou de graisse coûte 53 kJ et que la quantité d'énergie métabolisable du krill est de 3,5 kJ/g (Chappell *et al.* 1993b), pour compenser cette dette de 250 g, le manchot aurait dû ingérer 3,8 kg de krill en plus (pour un régime basé sur du krill à 100 %).

leur partenaire[16]. Par ailleurs, parmi les sept études, cinq ont été menées chez des oiseaux marins polaires : trois arctiques et deux antarctiques. Il est intéressant de constater que contrairement aux espèces antarctiques (pétrel antarctique, manchot Adélie), chez les Alcidés arctiques (guillemot de Brünnich, guillemot de Troïl, mergule nain), les parents compensent la déficience de leur partenaire. Il serait intéressant de distinguer si cela est à relier aux traits d'histoires de vie des différentes espèces ou alors si l'environnement arctique permet une plus grande flexibilité de l'effort parental chez les oiseaux marins (par exemple, le coût de la recherche alimentaire est peut-être moindre en Arctique qu'en Antarctique du fait d'une plus grande prédictibilité des proies). Pour cela, il serait possible d'étudier le comportement parental d'espèces proches se reproduisant aux deux pôles (ex : grand labbe *Catharacta skua vs.* skua antarctique *Catharacta maccormicki*, fulmar boréal *Fulmarus glacialis vs.* fulmar antarctique *Fulmarus glacialoides*, sterne arctique *Sterna paradisaea vs.* sterne antarctique *Sterna vittata*).

Trois des publications concluant à un comportement de compensation de la part du partenaire, présentent un paramètre direct de compensation (augmentation du niveau d'approvisionnement ; Tableau 6) et deux présentent un paramètre indirect (perte de masse accentuée ; Tableau 6), en considérant que la perte de masse de l'adulte reflète un plus grand effort pour nourrir les poussins du fait d'un approvisionnement plus fréquent et d'une proportion plus importante de nourriture accordée aux poussins plutôt qu'à la maintenance de l'adulte. Selon la théorie des traits d'histoire de vie, cela peut sembler assez paradoxal dans la mesure où l'on s'attend à ce que les oiseaux longévifs donnent la priorité à leur propre maintenance aux dépens de leur progéniture et donc maintiennent un niveau d'investissement fixe. Il est néanmoins possible que cette perte de masse provienne tout simplement du fait que ces oiseaux partenaires n'ont pas réussi à compenser au moins pour eux-mêmes la déficience de leur partenaire et que la perte de masse observée ne reflète en fait qu'une période de jeûne plus longue et non pas un comportement de compensation de la part des partenaires des oiseaux handicapés (Cf. paragraphe précédent). Il est dommage que les trois études montrant une augmentation du niveau d'approvisionnement de la part des partenaires, n'aient pas en même temps recherché une éventuelle perte de masse de ces mêmes partenaires. Encore une fois, d'après la théorie des traits d'histoire de vie, on peut s'attendre à ce que la condition corporelle des partenaires ne soit pas altérée, ce qui suggérerait que les oiseaux longévifs ne peuvent compenser pour une déficience de leur

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[16] Il faut tout de même nuancer cette surreprésentation des publications présentant un comportement de compensation de la part du partenaire ; l'existence d'un comportement de compensation étant certainement plus facilement publiable que l'absence d'un tel comportement.

partenaire qu'à la condition que leur propre maintenance et leur survie n'en soient pas affectées. Cette hypothèse est confortée par les études de Paredes *et al.* (2005) et Bijleveld & Mullers (2009) qui ont montré que les individus qui avaient compensé pour leur partenaire handicapé en augmentant leur niveau d'approvisionnement l'année N, présentaient un taux de survie l'année N+1 comparable à celui d'individus contrôles. Dans notre étude, il est probable que le coût occasionné par une éventuelle compensation aurait été trop important en terme de maintenance et de survie et que les conséquences à long terme auraient été proches de celles observées chez les individus handicapés (moindre survie des mâles, moindre fécondité des femelles l'année suivante). Ainsi, si l'on considère que le coût de la compensation du partenaire est proportionnel à l'intensité de la contrainte à laquelle l'individu handicapé est soumis, il est imaginable qu'une contrainte moins importante que celle exercée par notre handicap aurait pu conduire à un comportement de compensation de la part des partenaires. Cette hypothèse pourrait être confirmée en utilisant différents niveaux de contraintes (*i.e.* différentes tailles de handicap).

Tableau 6 : Récapitulatif des études ayant modulé l'effort parental chez des oiseaux longévifs en handicapant un des deux parents et ayant étudié les conséquences de cette contrainte sur le comportement du partenaire de l'oiseau handicapé.

Etude	Wanless *et al.* 1988	Sæther *et al.* 1993	Velando & Alonso-Alvarez 2003	Paredes *et al.* 2005	Harding *et al.* 2009	Bijleveld & Mullers 2009	Articles 1 et 5
Espèce	Guillemot de Troïl *Uria aalge*	Pétrel antarctique *Thalassoica antarctica*	Fou à pieds bleus *Sula nebouxii*	Guillemot de Brünnich *Uria lomvia*	Mergule nain *Alle alle*	Fou du Cap *Morus capensis*	Manchot Adélie *Pygoscelis adeliae*
Procédure expérimentale	Résistance hydrodynamique	Surpoids	Portance alaire diminuée	Surpoids, Résistance hydrodynamique	Portance alaire diminuée	Portance alaire diminuée	Résistance hydrodynamique
Augmentation de l'approvisionnement	Oui	-	-	Oui	-	Oui	Non
Distribution spatiale différente	-	-	-	-	-	-	Oui
Changement de régime	-	-	-	-	-	-	Non
Perte de masse	-	Non	Oui	-	Oui	Non	Non

III – Conséquences des deux contraintes pour la progéniture

II.1 – Résultats de cette étude

Tout d'abord, il faut rappeler que les poussins de manchots Adélie dépendent exclusivement de leurs parents dans la mesure où le nourrissage alloparental[17] est extrêmement rare chez cette espèce (Article 10 en annexe). Le succès reproducteur, en termes de nombre de poussins et de condition corporelle des poussins, traduit donc exactement le niveau d'investissement des deux parents.

Une fois de plus, la contrainte expérimentale a eu des effets plus sévères que la contrainte environnementale en ce qui concerne les poussins. Alors que la contrainte environnementale n'a eu aucun effet sur les poussins (Article 3), la contrainte expérimentale a eu pour conséquence de diminuer le succès reproducteur (lorsque les mâles étaient handicapés) ainsi que la masse de ces poussins (Article 1). Néanmoins, dans le cas des mâles handicapés, les effets délétères du handicap semblent davantage liés à une diminution de l'efficacité d'incubation (Article 2) ayant conduit à un succès d'éclosion moindre et probablement à une croissance altérée (Sockman & Schwabl 1998, Metcalfe & Monaghan 2001). Les conséquences du handicap sur les poussins, du fait uniquement de ses effets négatifs en mer sur les adultes (et non pas du fait des conditions d'incubation), ne sont donc certainement apparentes que chez les couples dont la femelle a été handicapée. Une diminution de l'approvisionnement des poussins par l'individu handicapé couplée à l'absence de compensation de la part de son partenaire a eu pour conséquence de diminuer de 40% la masse corporelle des poussins (Article 1). Du fait de leur moins bonne condition corporelle, il était à prévoir que les poussins des couples handicapés sollicitent plus leurs parents pour obtenir de la nourriture (Iacovides & Evans 1998) d'autant plus que la quantité de nourriture reçue par les poussins est positivement corrélée à leur niveau de sollicitations (Article 1). Les poussins de manchots Adélie pourraient donc *a priori* facilement faire tourner le conflit intergénérationnel en leur faveur. Or les poussins des couples handicapés n'ont pas augmenté leur niveau de sollicitations probablement parce que ce comportement leur aurait infligé un coût plus important (Verhulst & Wiersma 1997, Kilner 2001) que le bénéfice escompté (Article 1). Cela pourrait également expliquer pourquoi les partenaires des individus handicapés, ne disposant pas d'informations supplémentaires sur les besoins de leurs poussins, n'ont pas compensé la déficience de l'individu handicapé.

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[17] **Nourrissage alloparental** : nourrissage des jeunes par des adultes non-apparentés à ces jeunes.

II.2 – Comparaison aux données de la littérature

Dans quasiment toutes les études ayant mis en évidence un comportement de compensation de la part du partenaire, le succès reproducteur est resté inchangé, ce qui suggère que cette compensation a été efficace. Néanmoins, dans une des études ayant mis en évidence un comportement de compensation (Bijleveld & Mullers 2009), le succès reproducteur est diminué et trois autres études montrent que la masse corporelle des poussins est diminuée (Tableau 7). Ceci suggère que la compensation du partenaire, même si elle semble efficace en termes de succès reproducteur, n'est que partielle si l'on considère la masse des poussins. De manière surprenante, aucune autre étude que la nôtre ne s'est penchée sur le niveau de sollicitations des poussins alors que le comportement du poussin est susceptible d'affecter le comportement des parents (Kilner 1995, Roulin *et al.* 2000, Kitaysky *et al.* 2001) et notamment le comportement de compensation de la part de partenaires d'oiseaux handicapés.

Tableau 7 : Récapitulatif des études ayant expérimentalement modulé l'effort parental chez des oiseaux longévifs et ayant étudié la réponse des deux parents ainsi que les conséquences pour leur progéniture.

	Wanless *et al.* 1988	Sæther *et al.* 1993	Velando & Alonso-Alvarez 2003	Paredes *et al.* 2005	Harding *et al.* 2009	Bijleveld & Mullers 2009	Articles 1 et 2
Espèce	Guillemot de Troïl *Uria aalge*	Pétrel antarctique *Thalassoica antarctica*	Fou à pieds bleus *Sula nebouxii*	Guillemot de Brünnich *Uria lomvia*	Mergule nain *Alle alle*	Fou du Cap *Morus capensis*	Manchot Adélie *Pygoscelis adeliae*
Procédure expérimentale	Résistance hydrodynamique	Surpoids	Portance alaire diminuée	Surpoids, Résistance hydrodynamique	Portance alaire diminuée	Portance alaire diminuée	Résistance hydrodynamique
Diminution de la taille de ponte	-	-	-	-	-	-	Non
Diminution du succès d'éclosion	-	-	-	-	-	-	Oui
Diminution de la masse des poussins	-	-	Oui	-	Oui	Oui	Oui
Augmentation du niveau de sollicitations	-	-	-	-	-	-	Non
Diminution du succès reproducteur	Non	Oui	-	Non	Non	Oui	Oui

Parmi les études traitant d'une contrainte environnementale chez le manchot Adélie (Tableau 8), toutes ont montré que le manchot Adélie ne modifiait ni sa phénologie, ni sa taille de ponte en fonction des conditions environnementales. Par ailleurs, notre étude est la seule à ne montrer aucune conséquence négative sur le succès reproducteur en fonction des conditions environnementales (Article 3), confirmant à nouveau que la sévérité de la contrainte était moins importante dans notre étude que dans les autres.

Tableau 8 : Récapitulatif des études ayant examiné les conséquences de conditions environnementales différentes sur les poussins de manchots Adélie.

	Clarke *et al.* 2002 [a]	Nicol *et al.* 2008	Olmastroni *et al.* 2004	Watanuki *et al.* 1993	Clarke *et al.* 2002 [b]	Article 3
Localisation	Béchervaise Island	Béchervaise Island	Edmonson Point	Hukuro Cove	Béchervaise Island	Dumont d'Urville
Ponte retardée	Non	Non	Non	-	Non	Non
Diminution de la taille de ponte	-	Non	Non	-	-	Non
Eclosion retardée	-	Non	Non	-	-	Non
Diminution de la masse des poussins	Oui	Non	-	Oui	-	Non
Diminution du succès reproducteur	Oui	Oui	Oui	Oui	Oui	Non

[a] Données de Clarke *et al.* (2002) pour les années 1997 et 1998
[b] Données de Clarke *et al.* (2002) pour les années 1993 et 1994

IV – Mécanismes physiologiques associés aux deux contraintes

II.1 – Corticostérone et prolactine

Alors que la relation entre disponibilité alimentaire et corticostéronémie a été relativement bien étudiée chez les espèces arctiques (Buck *et al.* 2007, Kitaysky *et al.* 1999a, 2007), aucune donnée de ce type n'existe pour les espèces antarctiques. Ainsi, il a été décrit que les niveaux de corticostérone reflétaient le niveau de ressources alimentaires chez la mouette tridactyle *Rissa tridactyla* (Kitaysky *et al.* 1999a, Buck *et al.* 2007) et le guillemot de Troïl *Uria aalge* (Kitaysky *et al.* 2007). Cette relation a également été mise en évidence chez une espèce tempérée, l'hirondelle rustique *Hirundo rustica* (Jenni-Eiermann *et al.* 2008). Aucune des deux contraintes envisagées dans notre étude n'a conduit à une augmentation de la corticostéronémie pendant le stade de garde chez le manchot Adélie. A nouveau, il pourrait être intéressant de distinguer si cela est à relier aux caractéristiques des différentes espèces ou alors si les modifications environnementales en Arctique occasionnent un stress nutritionnel plus important chez les oiseaux marins (par exemple, les différences de disponibilité alimentaire sont peut-être plus marquées en Arctique). Pour cela, il faudrait tout d'abord pouvoir collecter et comparer davantage de données portant sur la corticostéronémie d'oiseaux antarctiques dans différentes conditions de disponibilités alimentaires et ensuite faire une étude comparative d'espèces proches vivant aux deux pôles, comme évoqué précédemment.

Par ailleurs, parmi les rares études ayant associé handicap et mesure de la corticostéronémie chez le parent handicapé, une seule étude (Harding *et al.* 2009)[18] sur cinq a pu mettre en évidence une augmentation des concentrations de cette hormone (Tableau 9). Cependant, cela ne signifie pas, dans les quatre autres études, que la corticostéronémie soit restée stable ; en effet, il se peut qu'au moment où la contrainte s'est exercée pour la première fois, les niveaux de corticostérone aient augmenté (Fig. 13, Suedkamp Wells *et al.* 2003) et aient redirigé le comportement des animaux (Landys *et al.* 2006) avant d'être régulés négativement.

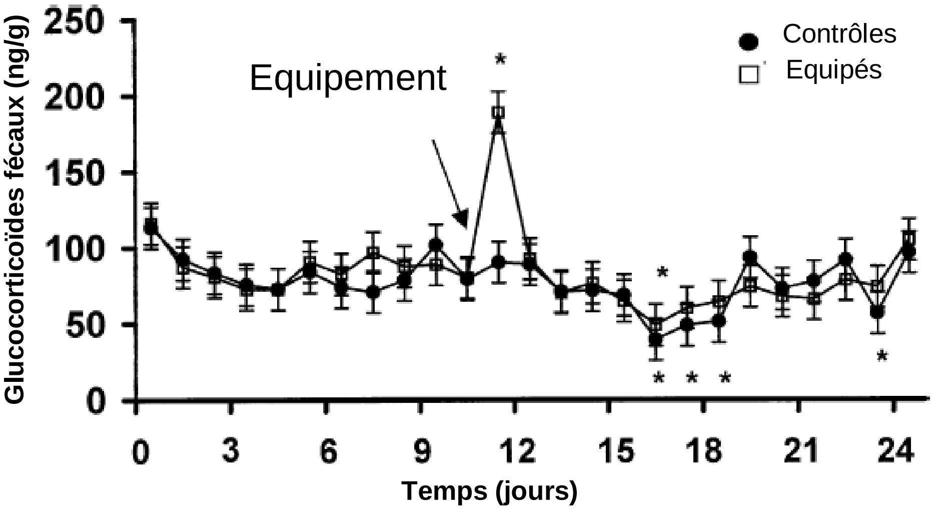

*Fig. 13 : Mesures des glucocorticoïdes fécaux de Dickcissels d'Amérique mâles (*Spiza americana*), contrôles (rond noirs) et équipés d'enregistreurs externes (carrés blancs). Les individus contrôles ont également été capturés mais n'ont pas été équipés. Les mesures ont été effectuées toutes les 24 heures. Les astérisques représentent des différences entre la mesure post-attachement et les niveaux pré-attachement (Suedkamp Wells* et al. *2003).*

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[18] Il est intéressant de noter que Harding *et al.* (2009) ont également mis en évidence une augmentation de la corticostéronémie chez les partenaires de mergules nains handicapés. Il est possible que le maintien d'une corticostéronémie élevée ait redirigé le comportement de ces individus, les incitant à augmenter leur effort de pêche et à compenser la déficience de leur partenaire handicapé.

Cette stratégie permettrait aux individus faisant face à une situation stressante d'éviter un état de stress chronique (Romero 2004). Il se peut que les guillemots de l'étude de Kitaysky *et al.* (2007) ainsi que les mergules nains handicapés de l'étude de Harding *et al.* (2009) ne soient pas parvenus à ajuster leur comportement pour éviter cet état de stress chronique. Au contraire, les manchots Adélie handicapés ou dans les différentes conditions environnementales de notre étude semblent être parvenus à adopter un comportement alternatif leur ayant permis d'échapper à ces situations stressantes (Wingfield & Kitaysky 2002), comme le suggèrent les changements dans la durée de leurs voyages alimentaires (Articles 1 et 3), leur distribution spatiale (Articles 3 et 5), leur comportement de plongée (Article 4) ou leur régime alimentaire (Article 3). Une étude de la cinétique des niveaux plasmatiques de corticostérone suite à une contrainte de reproduction et des changements comportementaux associés permettrait de confirmer cette hypothèse chez le manchot Adélie.

Par ailleurs, cette potentielle augmentation transitoire des niveaux de corticostérone aurait pu conduire à la diminution des niveaux de prolactine observés (Article 6). En effet, Angelier *et al.* (2009a) ont montré qu'une augmentation brève de la corticostéronémie conduisait à une diminution durable des concentrations plasmatiques de prolactine chez la mouette tridactyle. Chez les oiseaux, la prolactine induit et maintient l'expression des comportements parentaux. La diminution des niveaux de prolactine observée chez les femelles handicapées ou quand les conditions sont moins favorables, pourrait donc permettre aux parents de privilégier leur propre maintenance aux dépens de la reproduction en cours, par exemple en effectuant des voyages plus longs et donc en approvisionnant moins souvent les poussins (Article 6). De manière similaire, les abandons de la couvée (non observés dans notre étude) chez le manchot royal ont lieu chez des individus dont la condition corporelle est diminuée et sont associés à des niveaux de prolactine bas (Groscolas *et al.* 2008). Ceci est en accord avec les résultats de O'Dwyer *et al.* (2006) qui ont montré que les niveaux de prolactine étaient positivement corrélés à la condition corporelle de Pétrels de Gould *Pterodroma leucoptera*. Néanmoins, dans notre étude, les concentrations en prolactine étaient différentes en fonction de la contrainte environnementale alors que la condition corporelle des manchots ne différait pas entre les deux années (Article 3 et 6). Dans ce cas, une explication pourrait être que la prolactinémie serait plutôt liée au comportement que le manchot doit adopter pendant les voyages alimentaires pour garder une condition corporelle constante (Article 6).

Tableau 9 : Récapitulatif des études ayant modulé l'effort parental chez des oiseaux en handicapant un des deux parents et ayant étudié les conséquences de cette contrainte sur certains paramètres physiologiques de ces parents.

	Kern *et al.* 2007	Navarro & Gonzáles-Solís 2007*	Harding *et al.* 2009	Angelier *et al.* 2009c	Articles 5, 6 et 7
Espèce	Gobemouche noir *Ficedula hypoleuca*	Puffin cendré *Calonectris diomedea*	Mergule nain *Alle alle*	Manchot royal *Aptenodytes patagonicus*	Manchot Adélie *Pygoscelis adeliae*
Procédure expérimentale	Portance alaire diminuée	Surpoids	Portance alaire diminuée	Résistance hydrodynamique	Résistance hydrodynamique
Modulation des niveaux de corticostérone	Non	Non	Oui	Non	Non
Modulation des niveaux de prolactine	-	-	-	-	Oui (♀)
Modulation des niveaux de triglycérides	Non	Non	-	-	Non
Modulation des niveaux d'acide urique	Non	Non	-	-	Non
Modulation du statut oxydant	-	-	-	-	Oui

* complété par Navarro *et al.* 2008.

Enfin, pour tester la "motivation" des manchots à investir dans la reproduction actuelle ou dans leur maintenance, la réponse au stress des manchots handicapés, contrôles ou placés dans différentes conditions environnementales, aurait également pu être mesurée. Le principe repose sur le fait que la réponse au stress[19] est supposée diminuer en fonction du niveau d'investissement parental (Wingfield *et al.* 1995). En pratique, cela consiste à mesurer une première fois les valeurs basales de corticostérone et de prolactine et de mesurer une seconde fois ces mêmes hormones après un stress aigu (contention de l'animal pendant plusieurs dizaines de minutes). Un individu s'investissant dans la reproduction actuelle est supposé minimiser sa réponse au stress. A l'inverse, des individus s'investissant moins dans la reproduction actuelle et privilégiant leur maintenance devraient montrer une forte réponse au stress. Ainsi des mouettes tridactyles non reproductrices présentent une réponse au stress caractérisée par une diminution de la prolactinémie bien plus importante que chez des

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[19] **Réponse au stress** : chez les oiseaux, augmentation de la corticostéronémie et diminution de la prolactinémie.

individus reproducteurs (Chastel *et al.* 2005). On peut penser que les manchots handicapés présentant une masse diminuée et des poussins moins nombreux et plus petits (donc de moins bonne qualité) devraient privilégier leur maintenance au détriment de leurs poussins et donc devraient présenter une réponse au stress plus importante que celle de manchots contrôles. A l'inverse, on pourrait également s'attendre à ce que la réponse au stress soit minimisée chez les oiseaux handicapés du fait de la probable moindre sensibilité de leur axe hypothalamo-hypophyso-surrénalien (Müller *et al.* 2009), comme le suggère la faible corticostéronémie (et donc la probable régulation négative de la sécrétion de corticostérone) observée chez ces manchots (Article 5). Ces deux hypothèses demanderaient à être confirmées. Malheureusement, nous n'avons pas pu mettre en place ce protocole de stress de contention sur le terrain car nous voulions suivre les manchots sur le long terme. Or cette procédure, relativement traumatisante pour l'animal, aurait pu modifier son comportement *a posteriori*.

II.2 – Métabolites

Alors que la contrainte expérimentale semble avoir été plus sévère que la contrainte environnementale, seule la contrainte environnementale a conduit à une modulation des niveaux de métabolites. Ceux-ci sont difficiles à interpréter car dépendants de multiples facteurs : nature et composition de la proie, quantité de nourriture digérée, mobilisation des réserves endogènes, activité musculaire, etc. (Jenni-Eiermann & Jenni 1998). Par exemple, le fait que les niveaux de métabolites diffèrent uniquement pour la contrainte environnementale pourrait être dû au changement de régime alimentaire (contribution en poisson légèrement modifiée) observé pour la contrainte environnementale mais pas pour la contrainte expérimentale. Néanmoins le contenu protéique des deux principales espèces proies du manchot Adélie ne diffère pas véritablement (Tableau 11 en annexe) et ne peuvent expliquer les différences de concentration en acide urique. Par ailleurs, les niveaux de triglycérides étaient plus faibles lorsque la contribution en poisson, riche en lipides, était plus importante (Article 3). L'hypothèse expliquant le changement des niveaux des métabolites en fonction de la nature des espèces proies ne semble donc pas valable dans notre étude. Une autre hypothèse pourrait être que les concentrations en métabolites traduisent la quantité de réserves à mobiliser lors des voyages alimentaires. Ainsi la persistance de la glace associée à des niveaux de métabolites plus élevés, a possiblement nécessité la mobilisation de réserves plus importantes en forçant les manchots à effectuer des voyages plus longs et à prospecter dans des zones plus océaniques. Ainsi, Jenni-Eiermann & Jenni (1991, 1992) ont trouvé que pendant la migration, les passereaux présentaient des niveaux de triglycérides plasmatiques plus élevés, ceux-ci représentant une source d'énergie pour les muscles pectoraux lors du vol.

Les données disponibles dans la littérature au sujet des niveaux des métabolites chez des animaux handicapés ou dans des conditions environnementales différentes sont rares. Néanmoins, nous en avons trouvé trois dont les résultats sont en accord avec les nôtres (Tableaux 9 et 10). Dans aucun des cas, le handicap n'affecte les niveaux des métabolites (Kern *et al.* 2007, Navarro & González-Solís 2007) suggérant à nouveau que les animaux handicapés ont certainement ajusté leur comportement pour garder un état physiologique le plus stable possible (Cf. chapitre précédent sur la corticostérone et Article 5). Concernant la contrainte environnementale, nous n'avons trouvé qu'une seule étude ayant mesuré les niveaux de métabolites d'oiseaux reproducteurs dans des conditions environnementales différentes (Owen *et al.* 2005), et comme notre étude, cette étude montre que les niveaux de triglycérides et d'acide urique sont plus élevés lorsque les conditions sont les moins favorables. Clairement, les modifications des niveaux des métabolites en relation avec des modifications environnementales demanderaient à être approfondies et éclaircies, et ceci d'autant plus qu'il est tentant d'estimer la qualité d'un habitat entre autres, par la mesure des métabolites des animaux qui y vivent (Guglielmo *et al.* 2002, Owen *et al.* 2005).

Tableau 10 : Récapitulatif des études ayant examiné les conséquences de conditions environnementales différentes sur certains paramètres physiologiques chez des oiseaux adultes lors de la saison de reproduction.

	Owen *et al.* 2005	Kitaysky *et al.* 2007	Jenni-Eiermann *et al.* 2008	Articles 3, 6 et 7
Espèce	Moucherolle des saules *Empidonax traillii*	Guillemot de Troïl *Uria aalge*	Hirondelle rustique *Hirundo rustica*	Manchot Adélie *Pygoscelis adeliae*
Modulation des niveaux de corticostérone		Oui	Oui	Non
Modulation des niveaux de prolactine	-	-	-	Oui
Modulation des niveaux de triglycérides	Oui	-	-	Oui
Modulation des niveaux d'acide urique	Oui	-	-	Oui
Modulation du statut oxydant	-	-	-	Oui

II.3 – Stress oxydant

La distribution spatiale des manchots pendant leurs voyages alimentaires affecte de manière importante leur niveau de stress oxydant : les manchots réalisant des voyages alimentaires plus côtiers présentant un stress oxydant plus élevé (dommages oxydatifs plus élevés et capacité antioxydante diminuée, Article 8). Ceci est en accord avec les différences interannuelles que nous avons observées dans notre étude : les manchots prospectant dans des zones plus côtières en 2006-07 présentaient des niveaux de stress oxydant plus élevés que ces mêmes manchots prospectant dans des zones plus océaniques un an plus tard. Ainsi les manchots effectuant des voyages plus côtiers compromettent possiblement davantage leurs chances de survie, puisque le stress oxydant altère l'intégrité des télomères (von Zglinicki 2002, Richter & Von Zglinicki 2007) impliqués dans la sénescence (Bize *et al.* 2009). Aucune différence de survie l'année suivante n'a cependant été observée entre les deux années. Peut-être que ces différences n'apparaîtraient que sur une échelle de temps plus longue.

Cette relation entre distribution spatiale et stress oxydant n'a pas été observée chez les manchots handicapés très certainement parce que le handicap lui-même modifie le statut oxydant des manchots en augmentant leurs défenses antioxydantes (Article 7). Il est possible que cette augmentation leur ait permis de se prémunir contre des niveaux de ROS plus importants et donc contre les effets délétères des ROS sur des molécules clefs telles que l'ADN. Ainsi aucune accélération de la diminution de la taille des télomères chez les manchots handicapés n'a été observée, suggérant que l'augmentation des contraintes de reproduction *via* le handicap n'a eu aucun impact sur la sénescence des individus handicapés revenus se reproduire un an après l'expérimentation (Article 7).

Aucune donnée dans la littérature n'est disponible sur le stress oxydant et sur la dynamique des télomères d'oiseaux handicapés ou dans des conditions environnementales différentes. L'étude de Costantini *et al.* (2008) peut néanmoins être rapprochée de la nôtre. Leur étude a consisté à mesurer le statut oxydant de pigeons voyageurs ayant parcouru une distance courte ou une distance longue. Les pigeons ayant parcouru une distance longue présentaient des dommages oxydants augmentés et une capacité antioxydante diminuée. Ces résultats, opposés aux nôtres, pourraient provenir du fait que ces pigeons ont subi un effort aigu alors les manchots de notre étude ont subi une augmentation de l'effort de pêche de manière répetée (Radak et al. 2001). De plus, les animaux plongeurs sont sujets au problème d'ischémie/reperfusion (et donc à des concentrations très variables en oxygène au niveau des tissus) qui participe à la production de ROS (Hermes-Lima & Zentano-Savín 2002). En conséquence, les mammifères marins présentent une capacité antioxydante constitutivement élevée (Wilhelm Filho *et al.* 2002). Or, contrairement aux mammifères marins, chez le manchot Adélie, cette capacité antioxydante ne semble pas constitutivement élevée (comparable à celle du pigeon, Costantini *et al.* 2008) mais ajustable en fonction des contraintes de plongées. Cela pourrait passer par la surexpression de certains gènes (*e.g.* superoxyde-dismutase, catalase ou glutathion peroxydase ; Ogburn *et al.* 2001).

Un point à approfondir serait la dynamique du stress oxydant face à une contrainte. Par exemple, la mesure de stress oxydant dans notre étude (Articles 7 et 8) ne correspond qu'à une image instantanée du statut oxydant de l'animal après une période d'une journée environ sur le nid et avant qu'il ne reparte se réalimenter en mer. La capacité antioxydante étant supposée suivre les niveaux d'attaque oxydante, il est fort probable que la capacité antioxydante des manchot handicapés, plus élevée que celle des manchots contrôles, reflète une attaque oxydante plus élevée au moment où le handicap a augmenté l'effort de recherche alimentaire des manchots handicapés, c'est à dire pendant le voyage précédant la prise de sang. Il est donc probable que le niveau de dommages oxydatifs soit revenu à des niveaux basaux après une période au nid (Fig. 15). Les dommages liés à l'attaque oxydante (ROM) et la capacité antioxydante semblent donc présenter des cinétiques différentes. La capacité antioxydante des manchots handicapés apparaît plus persistante comme si ceux-ci restaient prêts à se protéger contre une nouvelle attaque oxydante lors du voyage alimentaire suivant. Une prise de sang au retour d'un voyage alimentaire suivie d'une prise de sang au départ du voyage alimentaire suivant permettraient d'éclaircir ce point (Fig. 15).

Un autre moyen d'étudier comment les contraintes de reproduction envisagées dans notre étude ont affecté le compromis entre maintenance et reproduction aurait été d'évaluer l'immunocompétence[20] des manchots sujets aux différentes contraintes. En effet, il a été montré chez les oiseaux qu'une augmentation expérimentale de l'effort reproducteur conduisait à une diminution de la production d'anticorps (Deerenberg *et al.* 1997, Ardia *et al.* 2003) ainsi qu'à une diminution de la réponse immunitaire à médiation cellulaire (Moreno *et al.* 1999). Cette diminution de l'immunocompétence pourrait être due à une production augmentée de ROS (Alonso-Alvarez *et al.* 2004) exerçant des effets délétères sur tous les tissus y compris le système immunitaire (Bendich 1996). Par ailleurs, l'augmentation de l'effort reproducteur accompagnée d'une diminution de l'immunocompétence des parents peut être suivie d'une diminution de la fécondité (Hanssen *et al.* 2005) et de la survie (Stjernman *et al.* 2004). Dans notre étude, du fait que la contrainte expérimentale a diminué la fécondité et la survie des manchots handicapés, on pourrait s'attendre à ce que ceux-ci présentent également une immunocompétence diminuée. Néanmoins, du fait de leur capacité antioxydante augmentée, les manchots handicapés auraient également pu se prémunir contre les effets délétères des ROS sur leur système immunitaire (tout comme sur leurs télomères) et auraient ainsi pu garder leur capacité immunitaire inchangée. Des études supplémentaires mesurant l'immunité acquise (ex : concentration d'immunoglobulines plasmatiques) et innée (ex : agglutination de globules rouges) pourraient donc être envisagées en complément des mesures de stress oxydant.

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[20] **Immunocompétence** : capacité de l'organisme à déclencher, maintenir et réguler une réponse immunitaire.

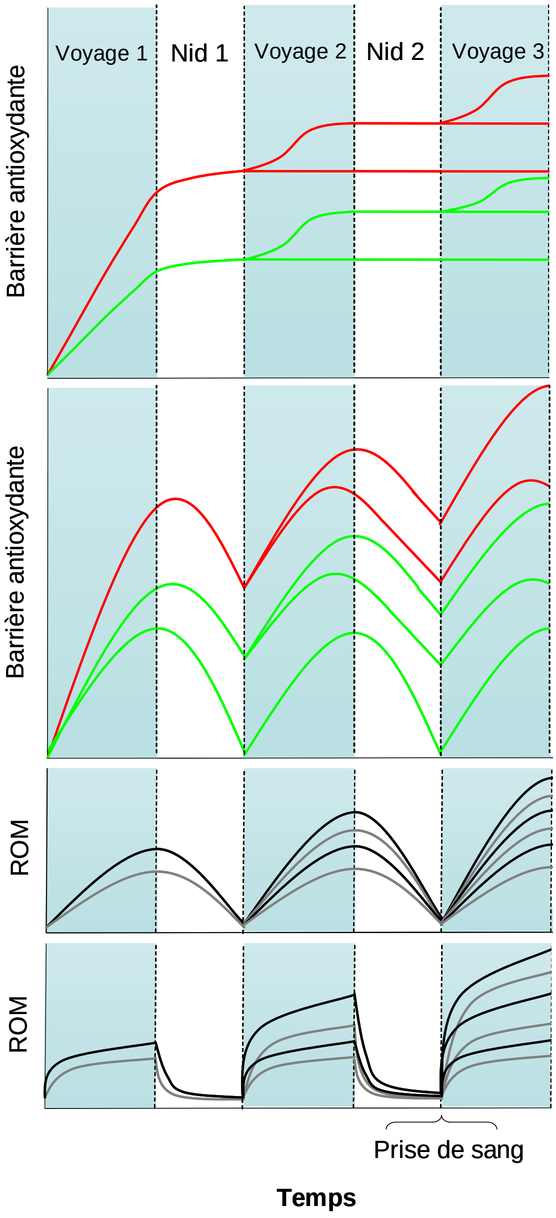

Fig. 14 : Schématisation des différentes cinétiques possibles pour les dommages oxydatifs (ROM) et la capacité antioxydante des manchots contrôles et handicapés. Ici, les manchots auraient effectué trois voyages alimentaires entrecoupés de deux périodes au nid. Courbe grise : ROM chez les manchots contrôles ; courbe noire : ROM chez les manchots handicapés ; courbe verte : capacité antioxydante des manchots contrôles ; courbe rouge : capacité antioxydante des manchots handicapés. La forme des différentes courbes est hypothétique.

IV – Conséquences à long terme

Seules deux études ont cherché à voir si l'augmentation des contraintes de reproduction chez un oiseau longévif handicapé avait des répercussions en termes de survie l'année suivante (Paredes *et al.* 2005, Bijleveld & Mullers 2009). Tout comme notre étude, Paredes *et al.* (2005) ont montré que l'augmentation expérimentale des contraintes de reproduction s'accompagnait d'une diminution du taux de retour des individus handicapés l'année suivant l'expérimentation (les mâles uniquement dans notre étude, Article 1), très certainement du fait d'une surmortalité. Cela montre bien que la procédure expérimentale a augmenté le coût de la reproduction. De manière opposée aux études de handicap, Wernham & Bryant (1998) ont "assisté" des couples de macareux moine *Fratercula arctica*, en nourrissant artificiellement leurs poussins. En réponse, les parents ont diminué leur niveau d'approvisionnement aux poussins. Les conséquences à long terme ont été opposées à celles de notre étude ; les parents "assistés" sont revenus en plus grand nombre l'année suivante et leur succès reproducteur a été supérieur à celui d'oiseaux contrôles. Ces deux types d'approche (handicap *vs.* assistance) montrent bien que le niveau d'investissement une année, aura de fortes répercussions sur la survie et/ou la fécondité des adultes l'année suivante.

Notre colonie d'étude fait toujours l'objet d'un suivi annuel pour connaître encore à plus long terme les effets de l'expérimentation sur la survie des manchots. Deux ans après l'expérimentation, le taux de retour des mâles handicapés était comparable à celui des mâles contrôles. Cela suggère que l'augmentation des contraintes de reproduction a conduit à l'élimination des mâles les moins performants[21] la première année (par exemple, les plus vieux) et donc à la sélection des mâles les plus performants l'année suivante (par exemple, les plus jeunes). Cette sélection ne s'est pas effectuée dans le groupe contrôle entre la première et la deuxième année, ce qui permet probablement d'expliquer pourquoi la mortalité dans le groupe contrôle a été plus importante que dans le groupe "mâles handicapés" entre la deuxième et la troisième année (Fig. 16).

Cette sélection des individus les plus performants est à prendre en considération dans la mesure où elle est susceptible d'avoir biaisé les mesures interannuelles effectuées sur les mêmes individus. En effet, l'approche consistant à sélectionner les mêmes individus année après année permet de s'affranchir de la variabilité interindividuelle mais en contrepartie, impose de ne considérer que les individus, probablement les plus performants, revenant se reproduire sur la colonie. Ainsi le fait que la dynamique des télomères reflétant la sénescence, ne soit pas accélérée chez les manchots handicapés (Article 7) est à prendre avec précaution dans la mesure où cela ne s'applique qu'aux individus de retour sur la colonie et donc certainement aux plus performants.

Tout comme chez les mâles handicapés, la procédure expérimentale a augmenté le coût de la reproduction chez les femelles handicapées qui ont diminué leur taille de ponte l'année suivant l'expérimentation. Néanmoins, contrairement aux mâles handicapés, le taux de retour des femelles handicapées est resté identique à celui des femelles contrôles un et deux ans après l'expérimentation (Fig. 16). De manière surprenante, les femelles des mâles handicapés (=femelles partenaires) ont vu leur taux de retour diminuer de manière

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[21] On considère ici un individu performant comme un individu reproducteur ayant été capable de minimiser l'impact négatif de la reproduction sur ses chances de survie et donc de retour l'année suivante sur le site de reproduction.

importante deux ans après l'expérimentation. Cela pourrait être dû au fait que bon nombre d'entre elles ont changé de partenaire l'année suivant l'expérimentation (Article 1) et qu'une saison de reproduction avec un nouveau partenaire pourrait être plus coûteuse qu'une saison de reproduction avec l'ancien partenaire. Néanmoins cette diminution du taux de retour des femelles partenaires semblait déjà s'amorcer un an après l'expérimentation et s'est accentuée par la suite. De plus, aucun paramètre un an après l'expérimentation ne suggérait que le coût de la reproduction était plus important chez les nouveaux couples que chez les couples stables (Article 1). Une autre hypothèse pourrait être que les femelles partenaires ont elles aussi supporté le surcoût occasionné par le handicap de leur mâle (par exemple par des périodes de jeûne plus longues) et que les conséquences de ce surcoût ne s'observent qu'à très long terme.

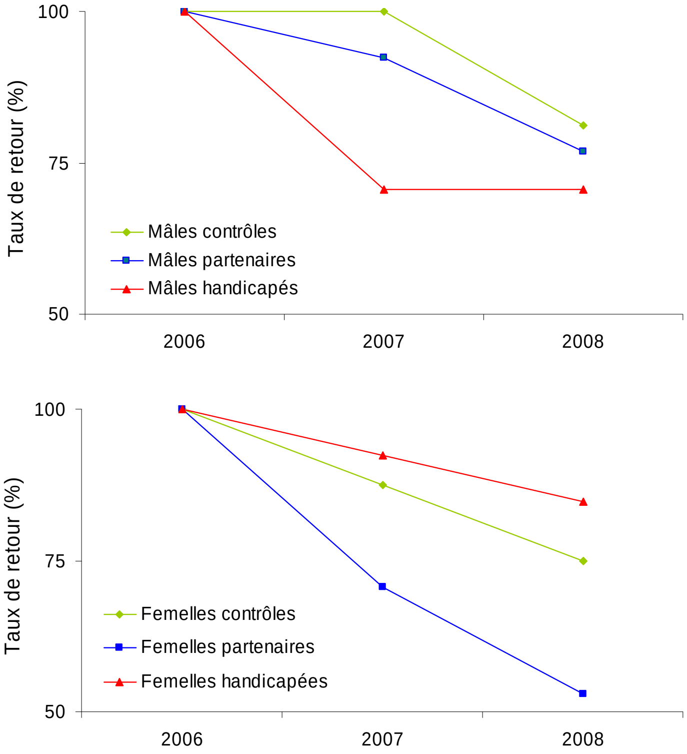

Fig. 15 : Taux de retour des manchots Adélie mâles (haut) et femelles (bas) un an (2007) et deux ans (2008) après la contrainte expérimentale.

Concernant la contrainte environnementale, le taux de retour des manchots contrôles était identique chaque année, confirmant ainsi que le niveau de contrainte exercé sur les manchots était bien inférieur pour la contrainte environnementale que pour la contrainte expérimentale.

Concernant les poussins, nous n'avons pas pu effectuer de suivi à long terme. Or on pourrait s'attendre à ce que la contrainte expérimentale ait des conséquences sur leur probabilité de survie et de reproduction. En effet, un poussin dont les conditions de croissance n'ont pas été optimales (comme les poussins des manchots handicapés), présente une probabilité de survie diminuée (Metcalfe & Monaghan 2001) et est susceptible de revenir se reproduire plus tardivement et de présenter une masse corporelle moindre lors des saisons de reproduction à venir (Gaston 2003). Par ailleurs, il aurait été intéressant d'examiner l'état physiologique des poussins pendant leur croissance, celui-ci étant susceptible d'affecter leur survie. Des prélèvements sanguins effectués sur les poussins auraient pu nous renseigner sur leur niveau de stress (*via* la mesure de corticostérone ; Harding *et al.* 2009, Kitaysky *et al.* 1999b, 2005, 2007), leur état nutritionnel (*via* la mesure des concentrations plasmatiques en métabolites, Jenni-Eiermann & Jenni 1998) et leur statut oxydant susceptible d'affecter leur survie (Bize *et al.* 2008). Harding *et al.* (2009) ont ainsi noté que les poussins de couples de mergules nains handicapés présentaient une corticostéronémie élevée. Par ailleurs, Navarro & González-Solís (2007) ont noté que l'immunocompétence des poussins de couples de puffins cendrés handicapés était également diminuée (possiblement du fait d'une corticostéronémie élevée (non mesurée)). Dans le cadre d'études à long terme, l'état physiologique des poussins pendant leur croissance pourrait être relié à leur probabilité de survie, à leur fécondité à venir et à leur capacité cognitive à l'âge adulte notamment lors de la recherche de nourriture (Kitaysky *et al.* 2006). L'état physiologique des poussins pourrait donc permettre d'anticiper leur survie et leur recrutement et donc les tendances démographiques à venir comme cela a déjà été proposé chez la mouette des brumes *Rissa brevirostris* (Kitaysky *et al.* 2006). Alors que plusieurs études ont relié disponibilité alimentaire et corticostéronémie chez les poussins d'oiseaux marins arctiques (Harding *et al.* 2009, Kitaysky *et al.* 1999b, 2005, 2007), pour l'instant, ces données manquent grandement chez les espèces antarctiques dont le manchot Adélie.

V – Conclusion générale et perspectives

Les différents tableaux présentés dans la discussion montrent que la plupart des études ayant modulé les contraintes de reproduction chez des oiseaux longévifs en handicapant un des deux parents, ne se sont généralement limitées qu'à l'individu handicapé en ne considérant qu'un nombre restreint de paramètres (durée des voyages alimentaires, perte de masse principalement, Tableau 4). Alors que toutes les espèces présentées dans ces études sont biparentales, seule la moitié de ces études a examiné les conséquences du handicap chez le partenaire et les poussins (Tableaux 6 et 7). De manière surprenante, aucune ne s'est intéressée aux facteurs proximaux susceptibles de moduler l'effort des parents tels que l'échange d'informations entre les partenaires d'un même couple (Houston *et al.* 2005, Johnstone & Hinde 2006) ou le niveau de sollicitations des poussins (Kilner 1995, Kitaysky *et al.* 2001, Roulin *et al.* 2000). Enfin, que ce soit pour la contrainte expérimentale ou pour la contrainte environnementale, très peu d'études se sont penchées sur la composante physiologique de l'investissement parental rendant la comparaison des résultats de notre étude avec d'autres données difficile (ex : métabolites) voire impossible (ex : prolactine). Ainsi, même si l'on arrive aujourd'hui à avoir une image des différentes réponses possibles des oiseaux longévifs face à différentes contraintes de reproduction, le couple représentant pourtant l'unité fondamentale des espèces biparentales (*i.e.* toutes les espèces d'oiseaux marins), ainsi que les mécanismes sous-jacents (comportementaux et physiologiques) régulant l'investissement parental, restent encore assez peu explorés. Enfin, les conséquences à long terme d'une augmentation des contraintes de reproduction telles que la survie ou la fécondité restent également très peu examinées (Paredes *et al.* 2005, Bijleveld & Mullers 2009), alors que l'étude de l'investissement parental (et donc de l'allocation des ressources entre reproduction et maintenance) implique que ce paramètre soit considéré.

En ce qui concerne notre étude, le manchot Adélie semble parfaitement se conformer aux hypothèses prédites par la théorie des traits d'histoire de vie : une augmentation importante et imposée des contraintes de reproduction induit une augmentation inévitable du coût de la reproduction se traduisant par une survie ou une fécondité diminuée l'année suivante. Ceci pourrait expliquer pourquoi aucun comportement de compensation n'a été observé de la part des partenaires des individus handicapés : s'ils avaient compensé, il aurait été probable qu'eux aussi auraient eu à en payer les conséquences en termes de survie ou de fécondité l'année suivante. Cependant ce schéma théorique (vérifié chez le manchot Adélie) ne semble pas être rencontré chez toutes les espèces longévives (Tableau 6) ; l'explication possible étant que les oiseaux longévifs ne peuvent compenser pour une déficience de leur partenaire qu'à la condition que leur propre maintenance n'en soit pas affectée. Cette hypothèse pourrait être examinée en vérifiant que le niveau de compensation éventuel du partenaire est proportionnel au niveau de contrainte imposé et que le comportement de compensation disparaît lorsque la contrainte devient trop importante (comme supposé dans notre étude). Pour cela, différents niveaux de contraintes seraient nécessaires, ce qui imposerait d'étudier un nombre très important de couples[22].

Même si nous n'avons pas pu mettre en évidence de comportement de compensation, il ne faut tout de même pas en conclure que le comportement des manchots Adélie pendant la saison de reproduction est figé. Comme le suggèrent les modifications comportementales des manchots suite à des variations environnementales (Article 3 et 4), le comportement parental des manchots Adélie tolère une certaine plasticité. Par ailleurs, contrairement à la contrainte expérimentale, cette plasticité semble n'avoir eu aucun coût en termes de condition corporelle ou de survie. Cela est vraisemblablement dû au fait que les niveaux de la contrainte expérimentale et de la contrainte environnementale étaient largement différents. Les relations prédites par Cairns (1987) entre le niveau de disponibilité alimentaire (modifiée par nos deux contraintes) et les conséquences induites chez les oiseaux marins confortent bien cette idée (Fig. 17) : le paramètre le plus sensible à une diminution de la disponibilité alimentaire étant l'effort de prospection alimentaire (dans notre étude, ce paramètre est modifié pour les deux contraintes) et le paramètre le moins sensible étant la survie des adultes (dans notre étude, ce paramètre est modifié uniquement pour la contrainte expérimentale). Dans ce contexte, il serait intéressant de déterminer à partir de quel niveau de contrainte, chaque paramètre (effort de prospection alimentaire, masse des poussins, succès reproducteur, survie) est altéré. Autrement dit, jusqu'à quel niveau de contrainte, la flexibilité comportementale des adultes permet-elle de ne pas avoir de conséquences sur le succès reproducteur et sur la survie des adultes.

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[22] Par exemple, notre étude comprenant 46 couples, n'a porté que sur un seul niveau de contrainte

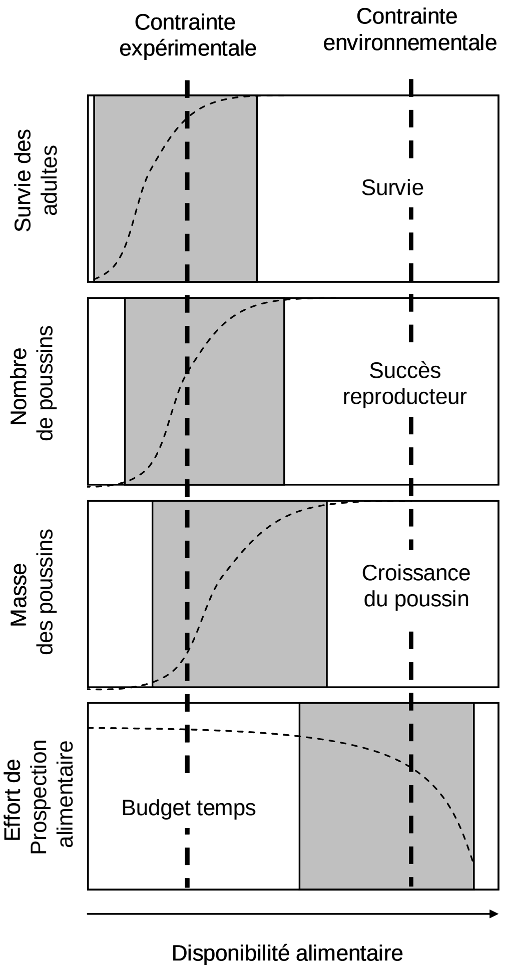

Fig. 16 : Relations prédites par Cairns (1987) entre le niveau de disponibilité alimentaire et les conséquences induites chez les oiseaux marins. Les lignes verticales en pointillés représentent les deux niveaux de contraintes présentées dans ce mémoire (inspiré de Piatt et al. *2007).*

En conclusion, malgré la complexité de la tâche, les études à venir traitant de l'investissement parental et donc de l'allocation des ressources entre reproduction et maintenance nécessiteraient d'intégrer l'ensemble des différents facteurs susceptibles de moduler l'investissement des parents (Fig. 1) et non pas de les considérer séparément. En effet, il est vraisemblable que ces différents facteurs interagissent. Par exemple, est-ce que la contrainte expérimentale aurait eu les mêmes effets chez l'individu handicapé, son partenaire et sa progéniture dans des conditions environnementales différentes ? Pour répondre à cette question, des études sur le long terme et incluant un très grand nombre d'individus seraient nécessaires.

5

ANNEXES

Annexes

Tableau 11 : Données bibliographiques portant sur la densité énergétique et les contenus lipidique et protéique des deux principales espèces proies du manchot Adélie (krill : Krill antarctique, Euphausia superba *et poisson : Calandre antarctique,* Pleuragramma antarcticum*).*

Euphausia superba	Densité énergétique (kJ/g masse humide)	Contenu lipidique (% masse humide)	Contenu protéique (% masse humide)	Remarques
Grantham 1977*		4,12	17,25	
Yanagimoto *et al.* 1979	4,86	6,90	13,60	
Clarke 1980		4,00	10,50	
Fik & Bartosiewicz 1981		3,53	15,87	
Shibata 1983		2,52		Dec.-Jan.
Clarke 1984		3,10		Jan.-Fev.
Reinhardt & Van Vleet 1986		1,30		
Reinhardt & Van Vleet 1986		6,30		
Reinhardt & Van Vleet 1986		8,60		Taille : 4.0-4.6 cm
Reinhardt & Van Vleet 1986		6,50		Taille : 3.4-3.6 cm
Hagen 1988		6,75		
Pond *et al.* 1995		1,81		Mâles
Pond *et al.* 1995		4,16		Immatures
Pond *et al.* 1995		3,48		Femelles
Phleger *et al.* 2002		1,45		Adultes
Phleger *et al.* 2002		1,46		Juvéniles de grande taille
Phleger *et al.* 2002		1,59		Juvéniles de petite taille
Barrera-Oro 2002	5,31			
Se-Jong & Rodger 2004*		5,05		
Moyenne ± écart-type	**5,10 ± 0,30**	**4,00 ± 0,50**	**14,30 ± 2,90**	

Pleuragramma antarcticum	Densité énergétique (kJ/g masse humide)	Contenu lipidique (% masse humide)	Contenu protéique (% masse humide)	Remarques
Reinhardt & Van Vleet 1986*		10,35		
Friedrich & Hagen 1994	4,84	10,20	11,70	Jan-Mars
Young 1994	6,40			
Robertson 1995*	7,47	8,97		Mars
Wöhrman *et al.* 1997*		8,03		
Hagen *et al.* 2000*		8,18		
Ainley *et al.* 2003	4.58			
Moyenne ± écart-type	**5,80 ± 1,30**	**8.90 ± 0,50**	**11,70**	

Lorsque les valeurs étaient données en gramme de matière sèche (*), nous avons considéré qu'*Euphausia superba et Pleuragramma antarcticum* étaient constitué de ~75% d'eau (Barrera-Oro 2002).

Article 9 : Investissement parental et sexe du poussin

SEX-SPECIFIC PARENTAL STRATEGIES ACCORDING TO THE SEX OF OFFSPRING IN THE ADÉLIE PENGUIN

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Sex-specific parental strategies according to the sex of offspring in the Adélie penguin

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In sexually dimorphic species, the sex of the offspring may induce different constraints for parents. At the same time, within pairs, males and females may have conflicting optimal reproductive strategies. As a result, they may adjust their level of parental investment differently according to the sex of the young. In this study, we examined whether Adélie penguin (*Pygoscelis adeliae*) chicks were sexually dimorphic and whether parents adjusted their parental investment accordingly. Male chicks were on average approximately 10% heavier than female chicks but not larger. Despite the presumed additional cost associated with male chick growth, no fitness cost differences were observed between parents rearing 1 chick whatever its sex: Adult body mass changes and resight rates during the subsequent breeding season were similar. However, the sex of offspring affected the duration of foraging trips during the early guard stage: At this stage, female adults rearing a female chick performed longer foraging trips than female adults rearing a male chick and males rearing either a male or a female chick. We propose that, because female adults present a lower survival rate after a breeding attempt, they are more prone to modify their level of parental investment than male adults. Moreover, the modulation of the foraging behavior by female adults according to the sex of the chick is likely to reduce intraspecific competition at a time when resource availability at sea is not optimal and when food requirement for female chicks may be lower than for male chicks. *Key words:* biparental care, foraging strategies, sex-related breeding effort. *[Behav Ecol 20:878–883 (2009)]*

Life history theory predicts that animals should balance the cost of their current reproduction against its potential negative effects on future reproductive attempts (Williams 1966). Parents are therefore expected to adjust their current investment according to resource availability, their own body condition, and their offspring need and value (Erikstad et al. 1997). In sexual size dimorphic species, when sexual dimorphism already exists in offspring, rearing a male or a female young may induce different breeding costs for parents (Cameron-MacMillan et al. 2007): Offspring of the larger sex may require more resources and therefore may incur additional reproductive costs. Moreover, if male and female offspring differ in their fitness value, parents should tolerate greater risks for offspring which is the most likely to survive and reproduce.

When both parents provide care to the young, males and females may have conflicting optimal reproductive strategies. In such a situation, who, from the male or the female, would take charge of this additional breeding cost? Different answers are conceivable: 1) both parents bear the additional cost (Weimerskirch and Lys 2000; Weimerskirch et al. 2000; Cameron-MacMillan et al. 2007), 2) male and female parental investment remains the same whatever the sex of the young (Lessels et al. 1998), and 3) only 1 parent modulates its investment according to the sex of the young. In this last case, the additional cost triggered by the larger offspring sex may generate sex-specific consequences on parents' body condition and survival: If consequences are too deleterious for 1 parent, it seems likely that this parent will not sustain the additional cost related to the larger young and will transfer this cost to its mate. Alternatively, interannual survival probability may differ between male and female parents: To maximize their lifetime reproductive success, individuals with high interannual survival should minimize their current reproductive effort at an optimal fixed level (Ricklefs 1987; Mauck and Grubb 1995). In contrast, individuals with a low interannual survival are expected to adjust the level of investment in their current reproduction at the expense of their own body condition.

Parents can modify their breeding effort by regulating provisioning rate toward offspring. For this purpose, they can adjust the duration of their foraging trips by alternating long and short foraging trips. It has been suggested that long foraging trips serve to enhance adult body condition at the expense of the offspring, whereas short trips enable the parents to provision the young at a high rate at the expense of the adult body condition (Weimerskirch 1998).

In this context, seabirds constitute a good model to examine sex-specific parental investment according to the sex of the young, as both parents provide care to the young (Gowaty 1996), they usually exhibit sexual dimorphism (Serrano-Meneses and Szekely 2006) and many species alternate short and long foraging trips (see Ropert-Coudert et al. 2004). Within seabirds, Adélie penguins (*Pygoscelis adeliae*) match these features: Males are larger than females (Ainley and Emison 1972) and during chick rearing, adults exhibit a bimodal distribution of foraging trip durations with short (15–25 h) and long (45–65 h) trips (Clarke et al. 1998; Clarke 2001). In addition, the interannual survival after a breeding attempt is higher in males than in females (Ainley and DeMaster 1980; Dugger et al. 2006): Consequently, female adults are expected to be more likely to modify their parental investment than male adults.

Until now, very few studies dealing with parental investment have taken into consideration simultaneously the sex of the parents and the sex of the young (Lessels et al. 1998; Weimerskirch and Lys 2000; Weimerskirch et al. 2000;

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Cameron-MacMillan et al. 2007). In this study, we checked whether sexual dimorphism was already present at the chick stage in Adélie penguins, then we tested the hypothesis that the level of parental investment depends on the sex of the parent and the sex of the chick. For this purpose, we analyzed parental provisioning decisions (foraging trip duration and feeding events) toward male and female offspring along the breeding cycle and investigated the consequences of the sex of the young on adult condition and survival.

MATERIALS AND METHODS

Study area and species

The study was conducted during 2 consecutive breeding seasons in Dumont d'Urville (66°40′S; 140°00′E), Adélie Land, Antarctica, during austral summers 2007–2008 and 2008–2009. In mid-November, female Adélie penguins lay 1 or 2 eggs. After hatching, males and females alternate foraging at sea and chick attendance at nest. This guard stage lasts from mid-December until mid-January. After 3–4 weeks, chicks get mobile and parents continue to feed their offspring sporadically for a few weeks until fledging (crèche stage, Figure 1). Adélie penguins feed mainly on krill (*Euphausia superba*, Ridoux and Offredo 1989) whose abundance, energy density, and distribution depend on the season (Clarke 1980; Nicol 2006).

Study protocol

We limited our fieldwork to pairs with only 1 chick from hatching till fledging so that the effects of offspring number and offspring sex are not confounded and the influence of sibling competition is excluded.

In 2007–2008, 32 pairs with only 1 chick were randomly selected within 1 colony to assess chick sexual dimorphism. Among these, 18 pairs were monitored more precisely to examine parental behavior: At the end of the courtship period, birds were captured on their nest and weighed with an electronic balance (Ohaus, ±2 g) and the left flipper (from the humeral head to the tip of the outstretched flipper) was measured with a ruler (±1 mm). Birds were identified with a Nyanzol-D mark painted on the breast feathers and with a subcutaneous passive transponder (Renner and Davis 2000). From the end of the courtship period until the end of the guard stage, these nests were observed from a distance every 2 h at worst and continuously at best to monitor copulation behaviors, laying, and foraging trip duration. Adult sex determination was carried out by a combination of parameters including cloacal inspection and copulation behavior and confirmed by examination of the incubation routine (Taylor 1962; Kerry et al. 1993). Adults were weighed a second time 40–45 days after laying when chicks were 7–10 days, while leaving the colony for a foraging trip.

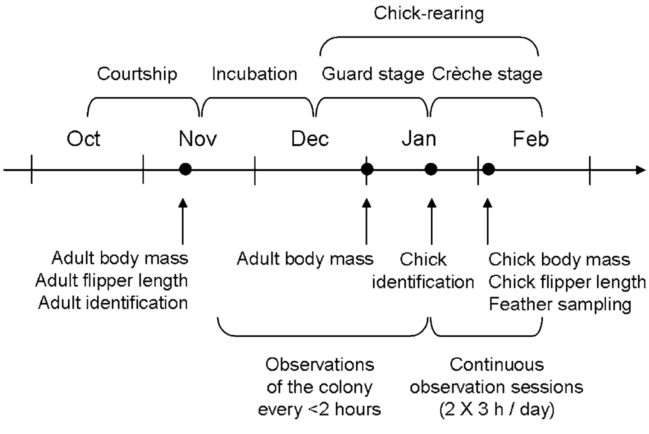

Figure 1
Breeding cycle of Adélie penguins (*Pygoscelis adeliae*) at Dumont d'Urville and study protocol.

During the crèche stage, it was impossible to obtain foraging trip durations by checking visually the presence of parents because they returned sporadically to the colony. To overcome this problem, the chicks were individually identified at the end of the guard stage with colored fish tags (FloyTag, Seattle, WA.) subcutaneously anchored in the neck. Each fish tag had a unique color code easily distinguishable from a distance. The colony was observed ad libitum, continuously with 8 × 20 binoculars from a blind overhanging the subcolony, about 20 m apart, and every parental feeding was noted. Observation sessions lasted 3 h every morning (0800–1100 h) and 3 h every afternoon (1500–1800 h) all along the crèche stage.

The 32 chicks were weighed on the colony with a spring balance (Salter, ±20 g) and their left flipper measured with a ruler (±1 mm) when they reached their maximum weight at 43–45 days (Ainley and Schlatter 1972). At the same time, 2 or 3 feathers were collected and stored at −20 °C for subsequent genetic sex determination (Figure 1).

In 2008–2009, the presence on the colony of formerly studied parents was checked with a manual antenna able to detect the subcutaneous transponder, during the courtship and the incubation periods.

Molecular sexing

Sex determination was carried out from an adapted protocol described by Kahn et al. (1998) and Ellegren (1996). DNA was extracted from feathers according to the method used by Sambrook et al. (1989). Polymerase chain reaction–based sexing was performed using the 1237L/1272H primer pair (Kahn et al. 1998).

Data analysis

We used flipper length as a body size indicator (De Leon et al. 1998; Minguez et al. 1998). A dimorphism index (DI; Storer 1966) was calculated for adults and chicks as: DI = (mean of females − mean of males)/[(mean of females + mean of males)/2] in which a negative result indicates that males are larger. As body mass was linearly related to wing length in adults (courtship: $F = 16.74$, $P < 0.001$; guard stage: $F = 28.05$, $P < 0.001$) and in chicks ($F = 9.77$, $P = 0.004$), we derived a body condition index from the residuals of a linear regression between the body mass and the flipper length (Green 2001; Benson et al. 2003; Schulte-Hostedde et al. 2005).

In adult penguins, flipper does not vary with time (Minguez et al. 1998) so that we were able to compare flipper length between chicks and adults and between males and females simultaneously. For this, we used a general linear model with the sex of the individual, the age class (chick or adult), and their interaction as fixed factors. In contrast, penguin body mass is highly variable according to the breeding stage (Vleck et al. 1999). For this reason, body mass analyses were compared in chicks and in adults independently. In chicks, sexual dimorphism for body mass was analyzed with a Student's *t*-test, whereas in adults, we used a general linear model with the sex of the adult, the sex of the chick, and their interaction as fixed factors (the same test was also used for adult flipper length). Changes in adult body mass were analyzed with a general linear mixed model with the number of the weighing (courtship and guard stage) as the repeated factor. A generalized linear model with a gamma distribution was used to compare foraging trip duration between groups. Because each individual did not perform the same number of foraging trips, we

Table 1

Sexual dimorphism for body mass and flipper length in Adélie penguin adults (n = 18) and chicks (n = 32)

		Male	Female	DI
Body mass (kg)	Adult	5.15 ± 0.11	4.49 ± 0.12	−13.71
	Chick	4.28 ± 0.14	3.89 ± 0.11	−9.55
Flipper length (mm)	Adult	198 ± 2	189 ± 2	−4.65
	Chick	190 ± 2	189 ± 2	−0.53

Results are presented as means ± standard error. DI = (mean of females − mean of males)/[(mean of females + mean of males)/2]. A negative result indicates that males are larger.

divided the guard stage into 3 substages (early, middle, and late), each of which comprising a third of the total number of foraging trips performed by an individual. A generalized linear model with a Poisson distribution was also used in the case of count data (number of feeding events during the crèche stage). Finally, resight rates were compared between groups using Fisher's exact tests. When necessary, multiple comparisons were undertaken using the post hoc Bonferroni test.

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL). Results are expressed as means ± standard error and significance level was set at $\alpha = 0.05$.

RESULTS

Sexual dimorphism in adults and chicks

Among the 32 pairs which reared only 1 chick between hatching and fledging, 14 had a male chick and 18 had a female chick.

Male adults were 0.7 kg heavier than female adults during the courtship period ($F = 16.84$, $P < 0.001$), and male chicks were 0.4 kg heavier than female chicks ($t_{27} = 2.16$, $P = 0.04$; Table 1). The age class and the sex of the individual affected flipper length ($F = 4.17$, $P = 0.04$): The flipper was 9 mm longer in male adults than in female adults ($P < 0.001$), but the flipper of male chicks was as long as the flipper of female chicks ($P = 0.56$). The flipper of female adults and that of female chicks were the same size ($P = 0.88$), whereas the flipper of male chicks was significantly smaller than the flipper of male adults ($P = 0.008$). Sexual dimorphism was more pronounced in adults: The chick DI for body mass represented 75% of the adult DI, and the chick DI for wing length represented 23% of the adult DI (Table 1).

During the crèche stage, male chicks were in a better condition than female chicks (body mass/flipper length residuals: 195.7 ± 4.5 g and −152.2 ± 4.6 g, respectively; $t_{28} = 2.15$, $P = 0.04$).

The sex of the chick was not related to the adult initial body mass ($F = 0.92$, $P = 0.35$), the adult flipper length ($F = 0.73$, $P = 0.40$; Table 2), and the adult initial body condition ($F = 0.32$, $P = 0.58$).

Breeding decisions from adults

In total, we analyzed 394 foraging trips: 199 performed by male adults and 195 performed by female adults. Foraging trip duration was 0.12 days (9%) shorter in males than in females (Wald's $\chi^2 = 15.02$, degrees of freedom (df) = 1, $P < 0.001$; Figure 2a). The sex of the chick also modulated the duration of the foraging trips performed by parents (Wald's $\chi^2 = 5.78$, df = 1, $P = 0.02$): Female adults rearing a female chick performed 0.15 days (11%) longer foraging trips than female adults rearing a male chick ($P = 0.02$). Female adults with a female chick also performed longer foraging trips than males, whatever the sex of the chick (all $P < 0.01$, Figure 2b).

The substages of the guard stage also influenced foraging trip duration (Wald's $\chi^2 = 29.13$, df = 6, $P < 0.001$). In the early substage, foraging trips performed by females rearing a female chick were 0.38 days (24%) longer than those performed by female adults rearing a male chick ($P < 0.01$) and longer than those performed by male adults (female chick: $P < 0.001$; male chick: $P = 0.01$). The duration of the foraging trips performed by female adults rearing a female chick decreased from 1.60 ± 0.10 days to 1.06 ± 0.04 days between the early and the late substages ($P < 0.01$). Females rearing a male chick performed foraging trips as long in the early substage (1.21 ± 0.04 days) as in the middle substage (1.36 ± 0.04 days, $P = 0.8$) but the foraging trip duration decreased in the late substage (1.09 ± 0.06 days, $P = 0.03$). Foraging trip duration performed by males rearing a male chick was constant along the guard stage (~1.2 days, all $P > 0.05$) and foraging trips performed by males rearing a female chick decreased only between the middle (1.33 ± 0.06 days) and the late (1.13 ± 0.06 days) substages ($P = 0.04$; Figure 2c).

During the crèche stage, male adults fed their chicks more than female adults although not significantly (5.25 ± 0.58 and 3.83 ± 0.49 feeding events, respectively; Wald's $\chi^2 = 3.50$, df = 1, $P = 0.06$), and the sex of the chick did not influence the number of feeding events by male and female adults (Wald's $\chi^2 = 0.11$, df = 1, $P = 0.74$; Table 2).

Adult body mass, body condition, and resight rate

Between the courtship period and the guard stage, body mass decreased similarly in parents (males or females) rearing a male chick and parents rearing a female chick ($F_{3,\ 27} = 1.14$, $P = 0.35$). In terms of percentage, male and female adults lost the same amount of body mass (10.21 ± 1.71%

Table 2

Characteristics of Adélie penguin parents classified according to the sex of the adults and the sex of the chicks

	Male adult (n = 18)		Female adult (n = 18)	
	Male chick	Female chick	Male chick	Female chick
Flipper length (mm)	197 ± 2	197 ± 3	191 ± 2	187 ± 3
Body mass during courtship (kg)	5.10 ± 0.17	5.21 ± 0.14	4.59 ± 0.19	4.39 ± 0.14
Body mass during the guard stage (kg)	4.61 ± 0.16	4.63 ± 0.11	4.33 ± 0.16	4.04 ± 0.11
Body mass loss (%)	9.44 ± 2.65	10.98 ± 2.16	5.42 ± 2.90	8.98 ± 2.45
Foraging trip duration in the guard stage (days)	1.21 ± 0.03	1.15 ± 0.04	1.23 ± 0.03	1.38 ± 0.05
Number of feeding events during the crèche stage	5.50 ± 0.96	5.00 ± 0.65	3.83 ± 0.80	3.83 ± 0.57
Resight rate in the next breeding season (%)	100	100	100	92

Results are presented as means ± standard error.

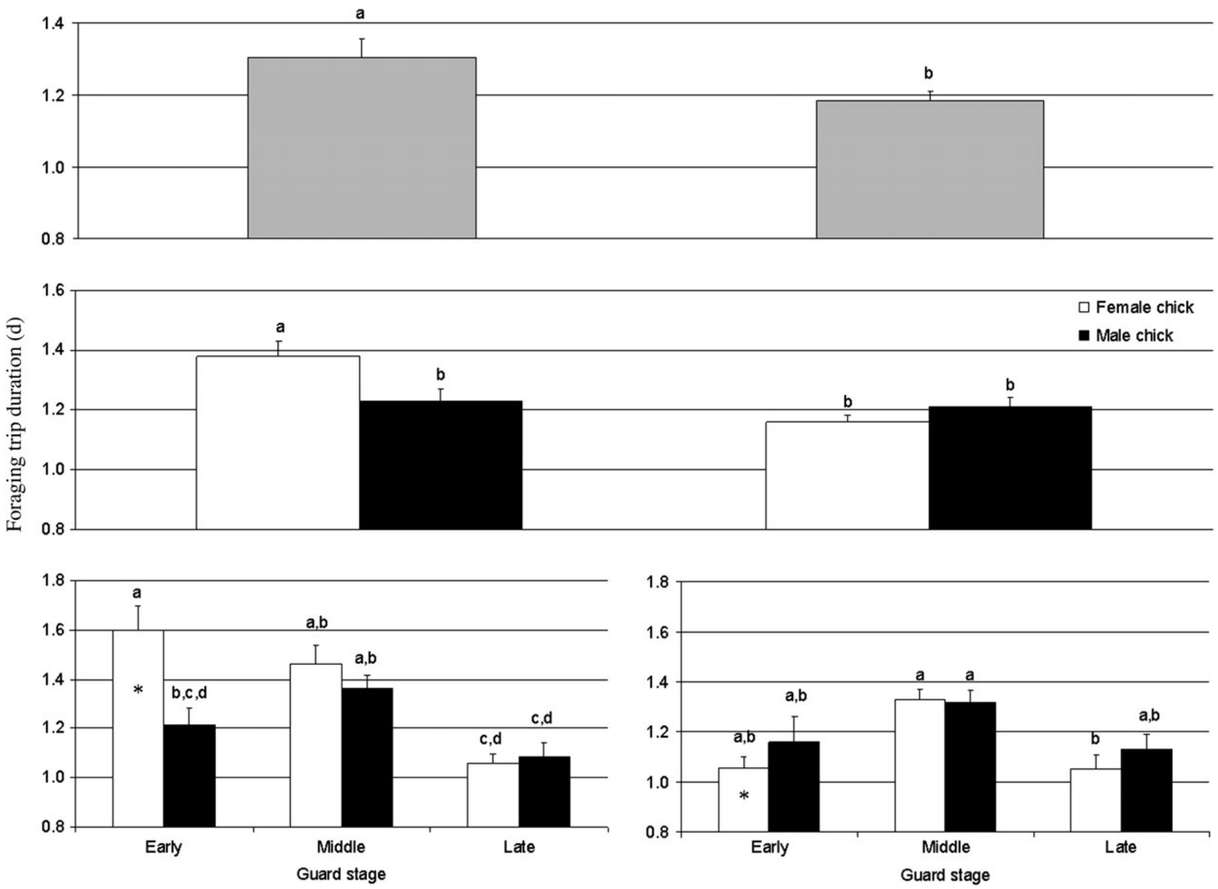

Figure 2
Foraging trip duration during (a) the guard stage in female and male adults; (b) according to the sex of the chick; (c) and in the early, the middle, and the late substages of the guard stage. Results are means ± standard error. Different letters indicate differences between substages and the chick sex for each parent. Asterisk indicates a significant difference between the male and female parents.

and 7.20 ± 1.90%, respectively; $F = 1.39$, $P = 0.25$) and this was not affected by the sex of the chick ($F = 1.55$, $P = 0.70$; Table 2). During the guard stage, the body condition of male and female adults was equivalent (body mass/flipper length residuals: 70.1 ± 79.4 g and −60.0 ± 78.2 g, respectively $F = 1.37$, $P = 0.25$) and the sex of the chick did not influence parental body condition neither in male adults nor in female adults ($F = 10.91$, $P = 0.35$).

Out of the 36 birds electronically identified in 2007–2008, 35 were resighted nesting in the colony during the subsequent breeding season. There were no differences in the resight rates of male or female parents rearing a male or a female chick 1 year before (Fisher's exact tests, all $P > 0.05$; Table 2).

DISCUSSION

In this study, sexual dimorphism has been described for the first time at the chick stage in penguins and we showed that parental foraging decisions were regulated by the sex of the young in female adults.

In chicks, the flipper length of female and male chicks was similar and was the size of the flipper of female adults. This indicates that female chicks had finished their statural growth, whereas male chicks had not reached their full adult body size before fledging. This suggests that parents sustained the whole cost associated with the statural growth of female chicks, whereas male chicks will have to sustain by themselves the remaining cost while fledged. For this, male chicks may be helped by their better body condition (compared with female chicks) at the end of the crèche stage.

Chick sexual dimorphism for body mass was close to sexual dimorphism observed in adults. Culik (1994) reported that a chick with a 3500 g body mass needs about 28.8 kg of food during its first 45 days. In our study, male chicks were about 400 g heavier than female chicks suggesting that male chicks would require 3.3 kg (11%) of food more than female chicks. Parents did not deduct this additional cost from their own reserves because they did not lose mass at a higher rate when rearing a male chick. This suggests that parents rearing a male chick sustained a higher effort at sea by catching more prey than parents rearing a female chick. In the case of poor resource availability, it is therefore expected that male chicks would be more susceptible to die from starvation, which could potentially lead to a female-biased sex ratio at fledging (Stamps 1990).

As previously described (Clarke et al. 1998), female adults performed longer foraging trips than male adults during the guard stage. Our results showed that this sex-specific foraging strategy was due to a change in the foraging decisions by female adults rearing a female chick during the early guard stage. As expected by the lower interannual survival probability reported in female Adélie penguins (Ainley and DeMaster 1980; Dugger et al. 2006), female adults were more likely to vary their level of parental investment. However, the difference in the survival of male and female adults is not sufficient to explain why only females modulate their foraging effort according to the sex of the young. In the wandering albatross

(*Diomedea exulans*, Weimerskirch et al. 2000) and in the common murre (*Uria aalge*, Cameron-MacMillan et al. 2007), both parents modify their provisioning behavior according to the sex of the young, whereas in these species, annual survival rate follow the same trend than that observed in Adélie penguins (Sydeman 1993; Nel et al. 2003). Moreover, we expected female adults rearing a female chick to acquire benefits from this situation, such as a lower body mass loss resulting in a better condition than that of female adults rearing a male chick. Nevertheless, this was not observed as the sex of the chick did not affect body condition or interannual survival of female adults.

As suggested by Clarke et al. (1998), the most plausible benefit seems to be a reduction of intraspecific competition between male and female adults. In early summer, krill availability is low (Siegel 2000) and is mainly constituted by individuals of low energetic density (Clarke 1980; Nicol 2006). Krill energy density increases when individuals and especially females become sexually mature. In Dumont d'Urville Sea, krill reproductive cycle begins late in summer, in late December–January (Spiridonov 1995). This suggests that between hatching (mid-December) and the end of December, that is, the early guard stage, adults rely on limited, poor resources. Intersexual competition may thus be the highest at this time of the breeding cycle and females with enough flexibility (i.e., with a female chick) may have to modify their foraging behavior by increasing foraging trip duration.

The difference observed in the behavior of female adults according to the sex of the chick progressively disappeared during the guard stage and at the end of the breeding cycle (middle and late guard stage and crèche stage), female adults behaved similarly toward male and female chicks. Because resource availability became greater and energetically more valuable at the end of the breeding cycle (Clarke 1980; Nicol 2006), intraspecific competition is likely to be reduced between male and female adults. Concurrently, growing chicks require more food (Culik 1994) thus obliging the parents to perform shorter foraging trips. Though not observed in male adults rearing a male chick, this trend was found from the early to the late guard stage in female adults rearing a female chick and from the middle to the late guard stage in female adults rearing a male chick and in male adults rearing a female chick.

In the present study, we were able to provide new insights in the understanding of the regulation of parental investment in long-lived birds according to the sex of the young. However, our findings raise new questions, especially about the recognition of the sex of the young by parents. As already demonstrated in other bird species (Teather 1992; Von Engelhardt et al. 2006), male and female chicks may beg for food differently, and although this has not been yet demonstrated in Adélie penguins, female adults may respond to the level of chick solicitations by adjusting foraging trip duration. Because female adults can perform longer foraging trips at the beginning of the guard stage when rearing female chicks but not male chicks, this suggests that chick requirements differ at this stage between male and female chicks. To elucidate this, further studies examining the growth rates of male and female chicks and the diet of adults according to the sex of the offspring are required.

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Article 10 : Nourrissage alloparental chez le manchot Adélie

ALLOPARENTAL FEEDING IN ADÉLIE PENGUINS:
WHY IS IT UNCOMMON?

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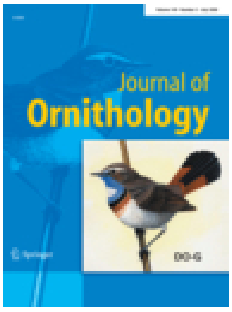

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ORIGINAL ARTICLE

Alloparental feeding in Adélie penguins: why is it uncommon?

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Abstract We investigated alloparental interactions and conditions which could facilitate or prevent the expression of alloparental behaviours in Adélie penguins (*Pygoscelis adeliae*), a long-lived seabird which nests in high-density colonies around Antarctica. Observation sessions were carried out during the crèche stage on 48 identified pairs and 50 identified chicks in a 217-nest subcolony. As the season progressed, young were fed less often by their own parents because these were increasingly absent from the breeding site and less responsive to their offspring's solicitations. As a consequence, young and particularly those with a low body mass, coming from a two-chick brood, opted for gradually soliciting more from other adults to obtain food, preferentially those nesting in their direct vicinity. Unsuccessful breeders represented a low and constant part of the adult population and were not specifically solicited by unrelated young. Despite the increasing chick demand, only 4.1% (3 out of 73) of alloparental solicitations resulted in feeding, which is negligible compared to parental feeding. To investigate factors that could trigger the appearance of alloparental care, we carried out comparisons with king (*Aptenodytes patagonicus*) and emperor penguins (*Aptenodytes forsteri*) which represent the closest species for which data on alloparental behaviour were available. Our results show different trends to those observed in these species and three factors may explain the low occurrence of alloparental behaviour in Adélie penguins: (1) the low and constant proportion of unsuccessful breeders, (2) the absence of chick selectivity towards unsuccessful breeders, and (3) the late period of chick accessibility for potential alloparents.

Keywords Alloparental care · Intergenerational conflict · Penguins

Introduction

Alloparental care (i.e. care of young by an unrelated adult) is inconsistent with life history theory: it is likely to incur fitness costs such as a decrease in adult survival (Rabenold 1990) or that of their offspring (Brown et al. 1995). An intergenerational conflict between unrelated young and adults is therefore predictable (Pierotti and Murphy 1987; Oro and Genovart 1999): young are expected to stimulate alloparental care while adults tend to restrain this behaviour (Brown 1998).

To explain this apparently paradoxical behaviour, several proximate facilitating factors can be proposed: (1) parental misrecognition (Brown et al. 1995), (2) high nest density (Saino et al. 1994) and proximity (Lecomte et al. 2006), (3) young accessibility, (4) young age and condition (Brown et al. 1995), and (5) breeding failure (Brown and Vleck 1998).

If alloparents can ultimately benefit from caring for unrelated young, alloparental care is likely to occur. In this context, several evolutionary hypotheses have been proposed: (1) kin selection when alloparental care is directed to closely related young, this can apply particularly in philopatric species (Riedman 1982), (2) reciprocal altruism when alloparents benefit from alloparental care for their

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offspring within one breeding season or over subsequent years (Pierotti 1982), and (3) acquisition of parental experience if parental care requires specific skills (Riedman 1982).

Alloparental behaviour has been described in many birds (Riedman 1982) and more specifically in long-lived birds (Arnold and Owens 1998) like seabirds (Birkhead and Nettleship 1984; Hebert 1988; Morris et al. 1991; Brown 1998). In penguins, alloparental care has been reported in three species: in little penguins (*Eudyptula minor*), 1.0–3.5% of chicks are fed by alloparents (Wienecke 1995); in emperor penguins (*Aptenodytes forsteri*), 7–15% of chicks are fed by alloparents (Jouventin et al. 1995); and in king penguins (*Aptenodytes patagonicus*), more than 65% of all chicks are fed by alloparents (Lecomte et al. 2006). These observations suggest that alloparental behaviour may exist in other species belonging to this order.

In penguins, the breeding period is divided into a guard stage and a crèche stage (Spurr 1975). Semi-altricial chicks are first constantly guarded at least by one parent while the other forages at sea to bring food back to its offspring. Alloparental care may occur during the guard stage in some species like emperor penguins where chicks are stolen from parents (Jouventin et al. 1995). In contrast, Adélie penguin (*Pygoscelis adeliae*) parents vigorously defend their nest during the guard stage and intruders are violently repelled. The only time when alloparents can have access to the chicks is when chicks are left unguarded during the subsequent crèche stage, when their demand for food requires both parents to forage simultaneously. During this period, adults return progressively less frequently to the subcolony until the end of the crèche stage when they permanently leave their breeding site. During the crèche stage, chicks get mobile and can walk away from their nest and consequently become accessible to potential alloparents. At that time, they have the option of waiting for irregular parent returns or seeking alloparental care and food from other adults.

All reported alloparental interactions in Adélie penguins were based on occasional observations (Crawford 1974; Spurr 1975). Nevertheless, proximate factors such as high density of colonies (suggesting close neighbour proximity), chick mobility and irregular parental returns during the crèche stage may favour alloparental care. In addition, ultimate factors mentioned above (kin selection, reciprocal altruism and acquisition of parental experience) may be supported by high natal philopatry (Ainley et al. 1995) and nest site fidelity (Williams 1995) in this long-lived species. Because of these features that may favour the occurrence of alloparental behaviour, we hypothesised that alloparental interactions should exist in Adélie penguins.

In this study, we investigated alloparental care and feeding in Adélie penguins and examined factors influencing the expression of this behaviour at the subcolony scale and from the perspective of both the chick and the adult.

Methods

The study took place in Pétrel Island (66°40′S, 140°00′E), Pointe Géologie Archipelago, Adélie Land, Antarctica, during the austral summer 2007–2008. The island holds about 15,000 pairs of Adélie penguins. In a 217-pair subcolony, 48 pairs were identified with a Nyanzol-D mark painted on the breast feathers during the courtship period.

The dimension of the subcolony, the number of nests and distances between nests were measured from an aerial photography taken vertically at the beginning of the season.

Breeding phenology for each pair was established by daily observations. A pair was considered as “unsuccessful” if parents lost their egg(s) during incubation or their chick(s) during the guard stage. At the end of the guard stage, all the chicks of identified adults were quickly sprinkled with paint (Raidex®) for recognition when they would be left unguarded for the first time. At this moment, they were weighed with a spring balance (Salter, ±20 g) and individually identified with coloured fish tags (Floy-Tag, Seattle, USA) subcutaneously anchored in the neck. Each fish tag had a unique colour code easily distinguishable from a distance. Chicks were weighed a second time when they reached their maximum weight at 43–45 days (Ainley and Schlatter 1972) and the fish tags were removed before fledging.

As soon as almost all the chicks were unguarded (mean date: 20 January 2008 ± 6.4 days, mean chick age: 28.1 ± 5.9 days), the subcolony was observed ad libitum, continuously with 8 × 20 binoculars from a blind overhanging the subcolony, about 20 m apart, during 3-h sessions every morning (0800–1100 hours) and every afternoon (1500–1800 hours) from 26 January to 8 February. First chicks fledged on February 10 so that our observations covered the major part of the crèche stage.

Before each session, photography of the subcolony was taken to evaluate demographic parameters: number of chicks, unknown adults, identified successful and unsuccessful breeders. Every behavioural interaction implicating at least one identified individual was noted. Three alloparental situations happened: “identified adult/identified chick”, “identified adult/unknown chick” and “unknown adult/identified chick”. We distinguished several interactions: (1) parental solicitation: when a chick begs for food to its own parent, (2) alloparental solicitation: when a chick begs for food to an unrelated adult, (3) parental feeding: when an adult regurgitates food to its own chick, and (4) alloparental feeding: when an adult regurgitates food to an unrelated chick. Feeding comprised several regurgitations and was scored as complete when no interaction between the adult and the chick occurred for at least 5 min (Dee Boersma and Davis 1997). A solicitation was considered as successful if it resulted at least in one regurgitation. Alloparental interactions unrelated to solicitations or feeding were also noted.

Demographic and behavioural trends during the study period were assessed with Spearman Rank correlations. The number of individuals was calculated for each session whereas behavioural rates were calculated on a daily basis (morning + afternoon). Student's *t* test was used to compare means and χ^2 or Fisher's exact tests to compare frequencies. Results are expressed as mean ± SD. Statistical analyses were performed on SPSS 14.0. All tests were two tailed with significance level set at $\alpha = 0.05$.

Results

Subcolony features and demographic parameters

The studied subcolony was 153 m^2 and contained 217 nesting pairs, resulting in a density of 1.42 nest/m^2. Its longest length was 18 m and its longest width was 13 m.

At the beginning of the crèche stage, among the 48 identified pairs, 10 (20.8%) had 2 chicks, 30 (62.5%) had 1 chick and 8 (16.6%) were unsuccessful (5 pairs lost their eggs during incubation and 3 pairs lost their chicks during the guard stage). Along the crèche stage, the total number of identified adults decreased (Fig. 1a) but the ratio between unsuccessful and successful breeders present in the subcolony remained unchanged (18.9 ± 5.5%; Spearman correlation, $r = 0.93$, $P < 0.01$). Only one chick

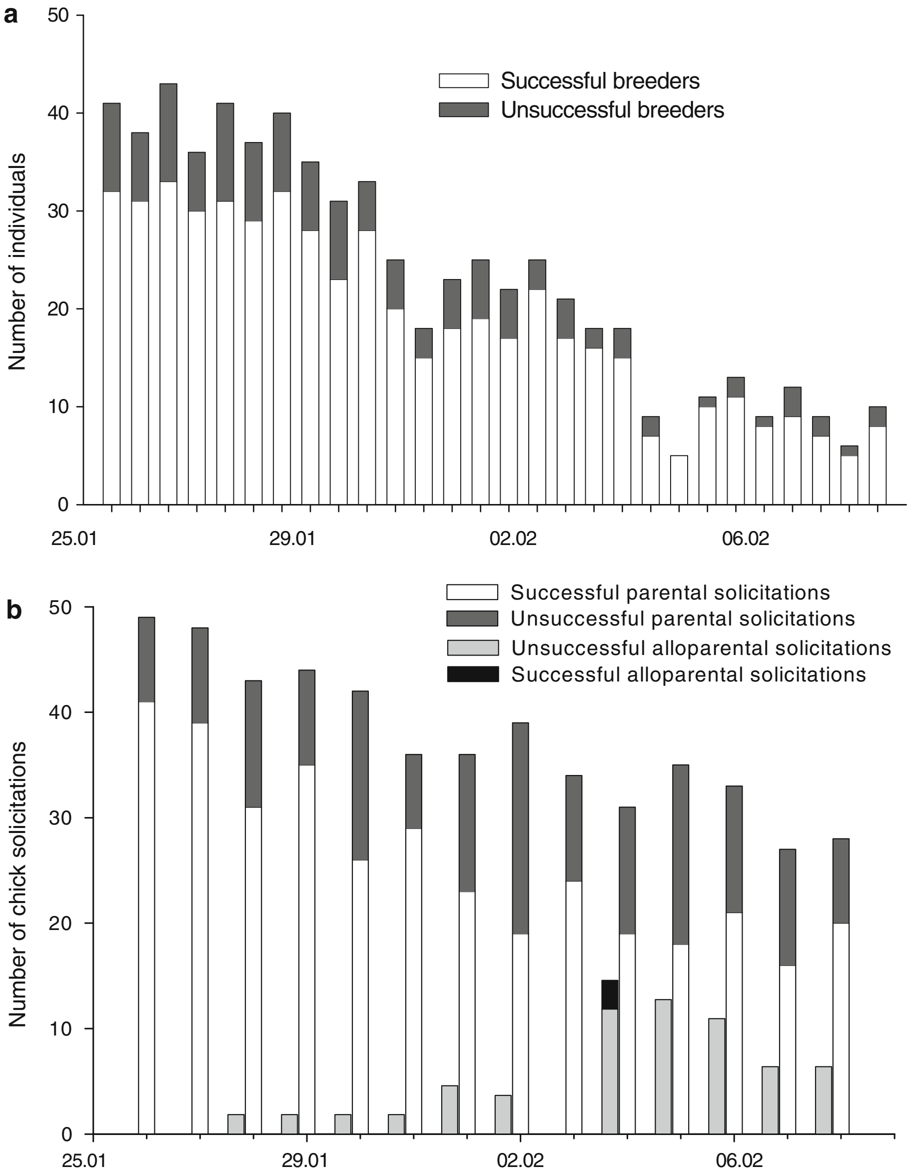

Fig. 1 Changes in the number of successful and unsuccessful Adélie penguin (*Pygoscelis adeliae*) parents observed in the subcolony (**a**) and in the number of parental/alloparental solicitations (**b**) during the crèche stage

coming from a 2-chick brood died by skua predation and no pair became unsuccessful during the crèche stage.

The 50 identified chicks belonging to the 48 identified pairs represented 30.3% of the 165 chicks present in the subcolony.

Solicitations and feedings

During the crèche stage, parental solicitations and feedings decreased by half (Fig. 1b). As the number of successful parental solicitations decreased, the number of unsuccessful parental solicitations increased (Spearman correlation, $r = -0.52$, $P = 0.05$). As a result, the proportion of unsuccessful parental solicitations progressively increased (Spearman correlation, $r = 0.65$, $P = 0.01$; Fig. 1b).

At the same time, as parental solicitations decreased, alloparental solicitations became gradually more important (Spearman correlation, $r = -0.72$, $P < 0.01$; Fig. 1b). However, over the whole study period, only 3 out of the 73 alloparental solicitations (4.1%) resulted in feedings (Fig. 1b), accounting for 0.8% of total feedings. One chick was fed by an alloparent twice and the other chick only once. The resulting proportion of chicks fed by alloparents was 4% (2 out of 50).

Young implicated in alloparental interactions

Sixty-four alloparental solicitations from identified chicks were observed; 46 (71.9%) implicated chicks coming from a two-chick brood. A significantly higher proportion of young coming from a two-chick brood (80.0%) solicited unrelated adults compared to single chicks (26.6%; Fischer exact test: $P = 0.007$). The three observed alloparental feedings occurred between unknown adults and two different identified chicks, each coming from a 2-chick brood. Only three cases of siblings competing while soliciting an unrelated adult were observed.

Young coming from a 2-chick brood had a significantly lower body mass than single chicks at the end of the guard stage (1,579 ± 156 g vs. 2,639 ± 141 g, respectively; Student's t test, $t_{48} = 4.935$, $P < 0.001$) and at the end of the crèche stage (3,525 ± 116 g vs. 4,120 ± 99 g, respectively; Student's t test, $t_{46} = 3.795$, $P < 0.001$).

Of the 30 alloparental solicitations observed between identified chicks and identified adults, 80% happened between individuals whose nests were less than 5 m apart (Fig. 2).

Adults implicated in alloparental interactions

Of the 39 alloparental solicitations, 15.4% observed between a chick and an identified adult were directed towards unsuccessful breeders, a proportion equivalent to the proportion of unsuccessful breeders in the subcolony (16.6%, $\chi^2 = 0.02$, $P = 0.88$).

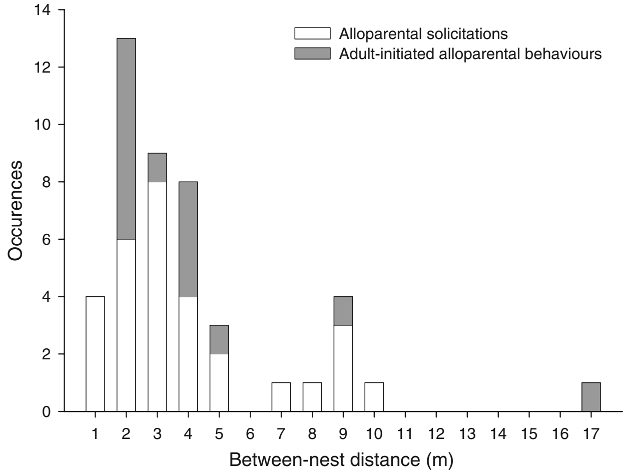

Fig. 2 Distribution of distances (m) between nests where identified chicks and identified adults implicated in alloparental interactions came from

Five types of adult-initiated alloparental behaviours were observed: (1) vocal displays ($n = 43$), (2) chick nibbling ($n = 21$), (3) chick pursuing ($n = 19$), (4) brooding attempts ($n = 16$), and (5) chick defending ($n = 6$). Among these adult-initiated alloparental behaviours, 15 occurred between identified chicks and identified adults. Thirteen (86.6%) happened between individuals whose nests were less than 5 m apart (Fig. 2).

Discussion

In Adélie penguins, as the crèche stage progressed, adult–young interactions partly shifted from the "parent–young" level to the "alloparent–young" level. These interactions resulted mainly from chick-initiated solicitations which were generally unsuccessful; allofeeding was highly uncommon and young clearly lost the intergenerational "arms race" (Brown et al. 1995).

Our results show different trends to those observed in the other penguin species in which alloparental care has been investigated. To explain such a discrepancy and investigate factors that could trigger the appearance of alloparental care in a long-lived species, a comparison of the situation between Adélie penguins and other penguin species seems worthwhile.

Subcolony features and demographic parameters

Our subcolony density (1.42 nest/m^2) was comparable to that of king penguins (1.6 incubating bird/m^2; Bauer 1967) in Crozet Archipelago where alloparental feeding was described (Lecomte et al. 2006). Consequently, even if high density facilitates contacts between unrelated individuals, it cannot be considered as determinative for alloparental feedings.

Alloparental feeding was described as most common among unsuccessful breeders (Jouventin et al. 1995; Lecomte et al. 2006). In our study, the proportion of unsuccessful breeders (16.6%) was comparable to the proportion in emperor penguins (11–20%; Jouventin et al. 1995) but was very low compared to that of king penguins: Lecomte et al. (2006) counted 76% of unsuccessful breeders during the crèche stage. Moreover, in king penguins, parents that had lost their chick during the crèche stage allofed more after the death of their chick than before. Lecomte et al. (2006) report that 43% of pairs failed during this period. In Adélie penguins, most failures occur during the incubation period or during the guard stage (Davis and McCaffrey 1986; Clarke et al. 2002; this study) and very few pairs become unsuccessful during the crèche stage. Consequently, this low and constant proportion of unsuccessful breeders in the subcolony resulted in a low and constant probability for a chick to ask for food to an unsuccessful adult along the crèche stage.

Comparing the number of chicks per pair and chick body mass in our study with data available in the literature (Marchant and Higgins 1990; Culik 1994; Watanuki et al. 1992; Watanuki et al. 1994; Janes 1997; Ainley 2002), we can assume that the year when observations for alloparental behaviour were carried out was similar to a classic year in terms of reproductive success (0.96 chick per pair in this study vs. 0.97 ± 0.31 chick per pair in the literature) and chick body mass (2,215 ± 904 g in this study vs. 2,458 ± 236 g in the literature; single chicks and chicks coming from two-chick broods, weighed at the same age or period). Therefore, it would be worthwhile conducting similar observations in years when breeding conditions differ and may modulate the frequency of occurrence of alloparental behaviours in Adélie penguins.

Young implication

The higher solicitation rate of young from two-chick broods towards unrelated adults cannot be due to sibling competition since siblings rarely solicited unrelated adults simultaneously. Chick condition is more likely the cause since young from two-chick broods presented a lower body mass which is known to increase begging (Iacovides and Evans 1998): Adélie chicks with a low body mass may present increased levels of baseline corticosterone (Walker et al. 2005) which facilitates begging towards adults (Kitaysky et al. 2000). This and the simultaneous decrease in parental feeding suggest that chick solicitations were driven by hunger and can, therefore, be considered as an honest signal from the chick to the adult.

Young actively solicited unrelated adults and their selectivity was oriented towards neighbours rather than unsuccessful breeders, which suggests that they waited near their nest and solicited any adult passing nearby.

Adult implication

As voice recognition is very effective in penguins (Spurr 1975; Davis and Mc Caffrey 1988; Jouventin and Aubin 2002), misrecognition is improbable and unrelated chicks are effectively recognized by adults. Nevertheless, as shown by adult-initiated alloparental interactions, adult Adélie penguins are interested in unrelated young. Since these alloparental behaviours were preferentially directed towards neighbour chicks, our findings are not opposed to reciprocal altruism and kin selection hypotheses, but data showing that offspring tend to breed near their parents in this species are still lacking.

Lecomte et al. (2006) report that allofeedings are more important at the beginning of the crèche stage in king penguins: adults seem to accept more easily feeding unrelated young chicks. As described for parental care (Varpe et al. 2004), alloparents may adjust their behaviour to the age of unrelated chicks as for emperor chicks who are adopted when they are 1–2 months, but not later, while they are still accessible (Jouventin et al. 1995, Fig. 3). Compared to king and emperor penguins, Adélie penguin

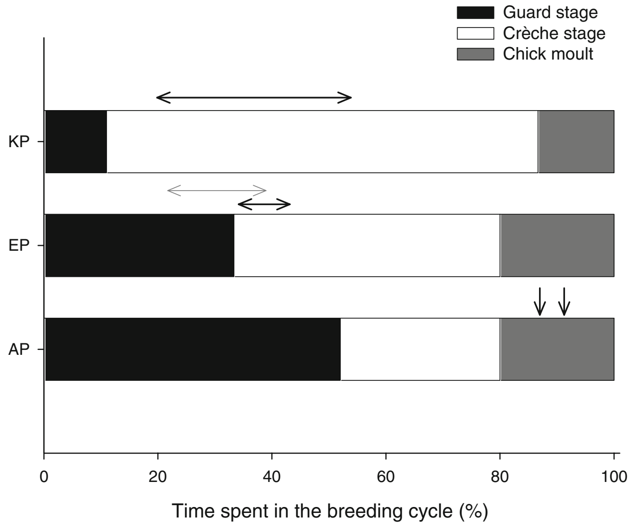

Fig. 3 Breeding phenology of king (*KP*) (*Aptenodytes patagonicus*), emperor (*EP*) (*Aptenodytes forsteri*), and Adélie (*AP*) penguins on a same time scale (breeding cycles were adapted according to data provided by Marchant and Higgins 1990). *Horizontal black arrows* indicate periods when allofeeding was described. *Horizontal grey arrow* corresponds to adoption period in emperor penguins. *Vertical arrows* indicate allofeeding occurence in our study

chicks are left unguarded and are accessible when they are older (Fig. 3), when they are probably less stimulating for unrelated adults. The stimulation that the chicks produce on the adult may also depend on the hormonal status of the adult. In emperor penguins, alloparental behaviour has been associated with persistent high levels of prolactin in failed breeders (Angelier et al. 2006). In contrast, at least in male Adélie penguins, prolactin levels were lower in unsuccessful parents than in parents still tending nests (Vleck et al. 2000). These low levels of prolactin might therefore partly explain the low occurrence of alloparental care in unsuccessful Adélie penguins.

To our knowledge, this article constitutes the first comprehensive study investigating alloparental feeding in Pygoscelids and provides the first data available in Pygoscelid species (Adélie, chinstrap *Pygoscelis antarctica* and gentoo penguins *Pygoscelis papua*). However, in the absence of data available in this genus, we were obliged to limit our comparison to king and emperor penguins. To improve our comparative approach, we invite other research teams to conduct similar studies and to publish their results even though alloparental behaviours are rare or absent in the studied species.

Zusammenfassung

Füttern durch Pflegeeltern bei Adeliepinguinen:
Weshalb ist es selten?

Wir haben Pflegeeltern-Interaktionen und die Bedingungen, welche die Äußerung von Pflegeelternverhalten ermöglichen oder verhindern könnten, bei Adeliepinguinen (*Pygoscelis adeliae*) untersucht, einem langlebigen Seevogel, der in dichten Kolonien um die Antarktis herum brütet. Beobachtungen wurden während des „Kindergarten"-Stadiums an 48 identifizierten Paaren und 50 identifizierten Küken in einer Subkolonie mit 217 Nestern durchgeführt. Mit fortschreitender Brutsaison wurden die Jungvögel weniger häufig von ihren eigenen Eltern gefüttert, da diese zunehmend vom Nistplatz abwesend waren und weniger auf das Betteln ihrer Nachkommen reagierten. Folglich bettelten die Jungvögel, und besonders solche mit geringer Körpermasse, die aus einer Brut mit zwei Küken stammten, mehr und mehr andere Altvögel an, um Futter zu erhalten, vorzugsweise solche, die in unmittelbarer Nähe brüteten. Erfolglose Brüter stellten einen kleinen und beständigen Teil der Altvogelpopulation dar und wurden nicht ausdrücklich von unverwandten Jungvögeln angebettelt. Trotz des steigenden Bedarfs der Küken führten lediglich 4,1% (3 von 73) der Bettelversuche bei Pflegeeltern zur Fütterung, was verglichen mit dem Füttern durch die Eltern unbedeutend ist.

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RESUME :

D'après la théorie des traits d'histoire de vie, toute augmentation de l'énergie allouée à la reproduction se fait au détriment de la survie et de la fécondité future des adultes. Par conséquent, les organismes longévifs se doivent de minimiser leur effort dans la reproduction actuelle de façon à maximiser leurs chances de survie et donc leur succès reproducteur tout au long de leur vie. Par ailleurs, chez les espèces biparentales, un conflit d'intérêt peut surgir entre les deux membres du couple puisque chacun des parents est censé minimiser son effort dans la reproduction actuelle.

Nous avons examiné le compromis entre reproduction et maintenance chez une espèce longévive et biparentale, le manchot Adélie *Pygoscelis adeliae*, lorsque les animaux doivent faire face à deux contraintes (expérimentale et environnementale) affectant l'accessibilité aux ressources alimentaires pendant la saison de reproduction. Quelle que soit la contrainte, les manchots Adélie changent leur comportement de recherche alimentaire : augmentation de la durée des voyages alimentaires en mer, modification de leur distribution spatiale et des paramètres de plongée. Ces modifications comportementales pourraient être la résultante de changements hormonaux (notamment de prolactine). Par ailleurs, les manchots privilégient leur maintenance en augmentant leur capacité antioxydante et semblent ainsi limiter l'impact négatif de la reproduction sur la sénescence de l'organisme (taille de télomères stable). Néanmoins, si la contrainte est trop importante, ces changements comportementaux et physiologiques sont insuffisants pour éviter une détérioration de leur condition corporelle, de leur taux de survie et de leur fécondité l'année suivante. Cela pourrait expliquer pourquoi, lorsqu'un seul membre du couple subit une forte contrainte, son partenaire n'augmente pas sa dépense parentale en réponse, probablement pour éviter les conséquences générées à long terme par un investissement trop important. La flexibilité du comportement parental chez le manchot Adélie apparaît donc limitée. Au delà d'un certain seuil de contrainte, cette flexibilité ne permet pas aux manchots d'échapper aux conséquences négatives de la reproduction sur leur maintenance.

Mots-clefs : contrainte de reproduction, compensation, compromis, corticostérone, couple, hormones, investissement parental, manchot Adélie, prolactine, recherche alimentaire, signature isotopique, stress oxydant, succès reproducteur, survie, télomères.

ABSTRACT: Résumé en anglais

Life-history theory predicts that an increased allocation of resources into current breeding will be followed by a lower adult survival or fecundity. Consequently, long-lived animals have to accurately regulate their effort in current reproduction to maximise their survival probability and lifetime breeding success. In addition, in biparental species, a conflict of interest may arise between mates, both being expected to minimise their breeding effort in current reproduction.

We examined the trade-off between reproduction and maintenance in a long-lived and biparental species, the Adélie penguin *Pygoscelis adeliae*, subjected to two constraints (environmental and experimental) affecting food accessibility during the breeding season. Penguins responded to both constraints by adjusting their foraging behaviour: longer foraging trips, modified spatial distribution and diving parameters. These behavioural changes are likely to result from hormonal changes (prolactin). In addition, penguins facing a breeding constraint give priority to their maintenance by increasing their antioxidant capacity, expected to reduce the negative impacts of reproduction on the organism senescence (steady telomere size). However, when the constraint is too severe, these behavioural and physiological adjustments are insufficient and in that case, penguins exhibit decreased body condition, lower survival rate and fecundity the subsequent year. This may explain why, when only one mate is subjected to a breeding constraint, its partner does not increase its parental effort to compensate, presumably to avoid the potential long-term consequences of an additional investment. In Adélie penguins, parental flexibility appears limited and beyond a threshold of constraint, this flexibility remains insufficient to avoid the deleterious consequences of reproduction on their fitness.

Keywords : Adélie penguin, breeding constraint, breeding success, compensation, corticosterone, foraging behaviour, hormones, oxidative stress, pair , parental investment, prolactin, isotopic signature, survival, telomeres, trade-off.