

Kidnapping of chicks in emperor penguins: a hormonal by-product?

Frédéric Angelier^{1,*}, Christophe Barbraud¹, Hervé Lormée², François Prud'homme¹ and Olivier Chastel¹

¹Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, and ²Office National de la Chasse et de la Faune Sauvage, F-79360 Villiers en Bois, France

*Author for correspondence (e-mail: angelier@cebc.cnrs.fr)

Accepted 31 January 2006

Summary

The function and causes of kidnapping juveniles are little understood because individuals sustain some breeding costs to rear an unrelated offspring. Here we focus on the proximal causes of this behaviour in emperor penguins (*Aptenodytes forsteri*), whose failed breeders often kidnap chicks. We experimentally tested the hypothesis that kidnapping behaviour was the result of high residual levels of prolactin (PRL), a hormone involved in parental behaviour. Penguins with artificially decreased PRL levels by bromocriptine administration kidnapped chicks less often than control penguins. Within the bromocriptine treated group, kidnapping behaviour was not totally suppressed and the probability of kidnapping a chick was positively correlated to PRL levels

measured before treatment. During breeding, emperor penguins have to forage in remote ice-free areas. In these birds, PRL secretion is poorly influenced by chick stimuli and has probably evolved to maintain a willingness to return to the colony after a long absence at sea. Therefore, penguins that have lost their chick during a foraging trip still maintain high residual PRL levels and this, combined with colonial breeding, probably facilitates kidnapping. We suggest that kidnapping in non-cooperative systems may result from a hormonal byproduct of a reproductive adaptation to extreme conditions.

Key words: kidnapping, hormones, prolactin, non-cooperative breeding, seabird, emperor penguin, *Aptenodytes forsteri*.

Introduction

Apart from a few species of cooperatively breeding animals, the function and causes of kidnapping juveniles are little understood (Wilson, 1975; Heinsohn, 1991). Why individuals struggle, feed and provide care for unrelated offspring is not clear (Riedman, 1982), and such kidnapping appears to be inconsistent with evolutionary theory (Riedman, 1982). However, some ultimate factors have been proposed to explain this strange behaviour. Firstly, kidnapping offspring could increase the kidnapper's breeding experience and hence promote their future breeding success (Riedman, 1982; Komdeur, 1996; Clutton-Brock, 2002). Secondly, because of their apparent breeding success and thus high individual quality, kidnappers could also enhance their probability of finding a mate for the next breeding event (Clutton-Brock, 2002). Finally, kidnapping can even create an association with the kidnapped offspring and thus enhance the probability of the kidnapper being helped during the subsequent breeding event (Heinsohn, 1991). Despite these potential benefits, kidnapping behaviour could also be costly because injuries could occur to the kidnapper if it tries to wrestle the offspring from its parents. Additionally, kidnapping of a chick may lead to costly parental behaviours because kidnappers might balance their need to

satisfy their own energy requirements with those of the kidnapped chick (Stearns, 1992; Heinsohn and Legge, 1999). Thus, ultimate factors arguably do not explain the kidnapping or adopting behaviour, except in some rare cases when the advantages outweigh disadvantages (Heinsohn, 1991). Consequently, kidnapping and adoption have sometimes been attributed to reproductive errors (Riedman, 1982; Birkhead and Nettleship, 1984; Bustamante and Hiraldo, 1990) resulting from failure to recognise the offspring.

Kidnapping behaviour could also be an artefact of proximate factors selected to allow reproduction in particular environmental conditions (Riedman, 1982). Among these proximate factors, hormonal mechanisms deserve particular attention, specifically prolactin (PRL), which is associated with parental physiology and behaviour in males and females (review in Buntin, 1996). PRL is also known to be associated with parental care provided by helpers in cooperative species (Vleck et al., 1991; Schoech et al., 1996; Brown and Vleck, 1998; Khan et al., 2001). Kidnapping of unrelated offspring could result from high residual hormone levels that are involved in the drive to provide parental care (Riedman, 1982; Birkhead and Nettleship, 1984; Jouventin et al., 1995). Although kidnapping behaviour has been described in many

species (Riedman, 1982), to our knowledge its proximate mechanism has never been experimentally studied.

In this study, we examined the physiological mechanism of kidnapping behaviour. We tested specifically for the effect of artificially decreased PRL levels on kidnapping behaviour in a non-cooperative species, the emperor penguin *Aptenodytes forsteri* Gray, where the kidnapping of chicks by failed breeders is commonly observed (Jouventin et al., 1995). In emperor penguins, ultimate factors could not explain kidnapping behaviour because in most cases kidnapers neglect the chick only a few hours after the kidnap (Jouventin et al., 1995), so that there do not seem to be any obvious advantages for kidnapers and kidnapped chicks. Emperor penguins thus constitute a promising model to study the proximate factor triggering kidnapping behaviour. In contrast to most bird species (Chastel and Lormée, 2002), penguins that lose their eggs or their chicks maintain high residual PRL levels throughout the whole breeding season (Garcia et al., 1996; Lormée et al., 1999; Vleck et al., 2000). We hypothesised that kidnapping behaviour is the result of these high levels of PRL. Therefore, we predict that penguins with experimentally decreased PRL levels would either stop kidnapping chicks or would kidnap them less often.

Materials and methods

Study area and species

We conducted our study from 20 August to 30 September, 1999, at Pointe Géologie archipelago, Terre Adélie, Antarctica (66°40'S, 140°01'E) on emperor penguins that breed in a colony near the Dumont d'Urville Station (Prévost, 1961). Emperor penguins breed during the Antarctic winter in dense colonies on sea ice. Monogamous pairs form in May, and following a 65 day incubation shift undertaken by the male alone, females come back to relieve their partner and bring food to the newly hatched chick. Then, both parents take turns to feed at sea and to stay with their offspring, until the chicks leave the colony when the sea ice breaks up (Prévost, 1961).

Kidnapping behaviour

Kidnapping behaviour is mostly exhibited by failed breeders, especially females, which have lost an egg or a young chick (Jouventin et al., 1995). During kidnapping, the biological parent always tries to protect the chick by fighting (pecking, stroke of flipper) the intruder (Jouventin et al., 1995), but kidnapers are sometimes able to displace the parent and to get the chick (Prévost, 1961). It is very rare that kidnapping episodes end in physical injury to the parent or to the kidnapper (H. Lormée, personal communication). Kidnapped chicks can sometimes benefit from being fed by the kidnapping parent, but in most cases kidnapers neglect the chick only a few hours after it was kidnapped, and the chick left unattended dies due to hypothermia or predation (Jouventin et al., 1995). 'Readoptions' of chicks by their parents are rare and occur only when the kidnapper rapidly abandons the chick, when the parent is still close to the chick and when the abandoned chick

calls its parent (Jouventin et al., 1995). Kidnapping mostly occurs during August and September. Failed breeders are very active during the weeks that follow the hatching period, when the presence of chicks may stimulate kidnapping behaviour (Prévost, 1961).

Manipulation of prolactin levels and prolactin assay

In winter 1999, 47 failed breeders were captured, individually marked by a number painted on their chest and 1 ml of blood was collected, prior to treatment, from the marginal vein of the flipper into heparinized tubes and then immediately centrifuged. Plasmas were stored at -20°C until measured for PRL concentration by radioimmunoassay as described (Lormée et al., 1999). Plasma PRL levels were experimentally decreased by treating the penguin with an intramuscular injection of bromocriptine (Parlodel^R long-acting form, Sandoz, Basel, Switzerland; 1.5 mg kg⁻¹ body mass). Bromocriptine is a dopamine agonist that inhibits PRL secretion in mammals (Bridges and Ronsheim, 1990; Roberts et al., 2001; Ben-Jonathan and Hnasko, 2001), and in birds (Jouventin and Mauget, 1996; Reddy et al., 2002). One group (bromocriptine group, *N*=23 birds) was treated with bromocriptine; the other (control group, *N*=24 birds) was treated with a vehicle (10% ethanol solution). The penguins were then released near the colony. We did not observe any adverse effect of bromocriptine on the behaviour of treated penguins and the sighting probability was similar between groups (no difference in sighting probability, see the Results section). Moreover, all treated penguins were seen later (at the end of the breeding season) in the colony.

To monitor the effect of bromocriptine treatment on PRL levels, we kept two additional birds (one injected with bromocriptine and one injected with a vehicle) in captivity and blood was sampled 3 days and 8 days after the capture. Afterwards, they were released back to the colony. All procedures used in this study were approved by the ethical institution of the French Polar Institute (IPEV). PRL levels were determined by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé (France) following the procedure previously validated for the emperor penguin and described in Lormée et al. (Lormée et al., 1999). Only one assay was performed and the intra-assay coefficient of variation was 3.5% (*N*=4 duplicates).

Behavioural monitoring and statistical analysis

We followed the kidnapping behaviour of the birds from the bromocriptine and control groups during a 3 h scan each day during the week following treatment. Hence we were able to attribute for each day and each monitored bird a categorical datum (sighted and non-kidnapped=non-kidnapping state; sighted and kidnapped=kidnapping state; or not sighted). A bird was classified as a kidnapper when he or she was in physical contact with the chick.

To model the kidnapping behaviour, daily resighting data obtained for each individual were analysed using multistate probabilistic models (MARK software, White and Burnham,

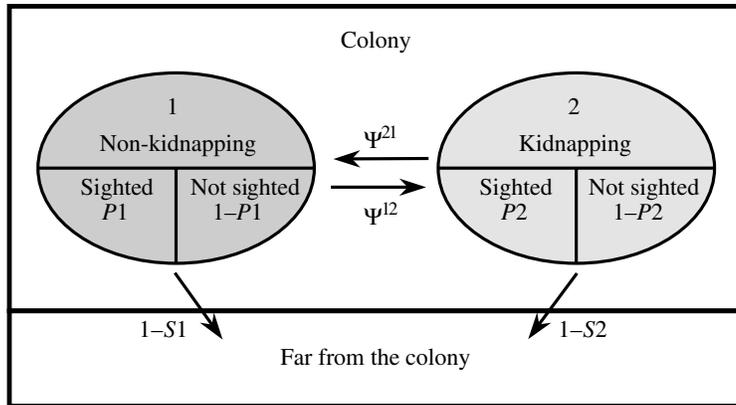


Fig. 1. Modelling kidnapping behaviour with a multi-state approach in the emperor penguin. States 1 and 2 are, respectively, the non-kidnapping state and the kidnapping state. Ψ^{ab} is the transition probability from state a to state b over one post treatment day (t) to the next one ($t+1$). Ψ^{12} is the probability that a penguin will kidnap a chick from t to $t+1$. $(1-S)$ is the probability that a bird will leave the colony from t to $t+1$. P and $(1-P)$ are, respectively, the probabilities that a bird present on the colony in one of the behavioural state was seen or not during the daily scan.

1999). These models include three kinds of parameters: sighting probability, survival probability and transition probabilities from one state to another (Nichols et al., 1994). We used two states in our study: (1) birds present but not seen kidnapping, and (2) birds seen kidnapping (Fig. 1). Contrary to classical statistical tests, this modelling approach permits independent estimates of kidnapping and resighting probabilities, hence providing a better estimate of the treatment effect on the kidnapping behaviour of emperor penguins (Lebreton et al., 1992) by taking into account the probability of sighting of the bird. We focused mainly on the probability of transition (Ψ) from the non-kidnapping state to the kidnapping state over one post-treatment day (t) to the next ($t+1$). This allowed us to estimate the kidnapping probability of failed breeders, and to test for an effect of bromocriptine treatment on the kidnapping behaviour of these birds. In our study, the apparent survival probability (S) represents the probability that an individual survived and stayed on the colony from one post-treatment day (t) to the next ($t+1$). Note that because all birds survived (they were seen later in the breeding season), S did not measure the survival probability *per se*. $(1-S)$ represents the probability that a penguin left the colony from one post-treatment day (t) to the next ($t+1$) and did not come back before the end of the behavioural monitoring period (Fig. 1).

An effect of treatment on survival probability means that bromocriptine-treated and vehicle-treated penguins have not the same probability to stay on the colony from one day (t) to the next ($t+1$). An effect of state (kidnapping or non kidnapping) on survival probability means that kidnapping and non-kidnapping birds during the post-treatment day (t) differ in the probability of staying on the colony from this day (t) to the next ($t+1$). The sighting probability (P) represents the probability that an individual was seen during the daily 3 h scan of the post-treatment day (t), given that it is alive and present on the colony during this post-treatment day (t). $(1-P)$ represents the probability that an individual was not seen during the daily 3 h scan of the post-treatment day (t) given that it is alive and present on the colony during this post-treatment day (t). An effect of treatment on sighting probability means that bromocriptine-treated and vehicle-treated penguins

differ in the probability of being seen during a post-treatment day (t), given that they are alive and present on the colony during this day (t). An effect of state (kidnapping or non kidnapping) on capture probability means that kidnapping and non-kidnapping penguins have not the same probability of being seen on the colony during the post-treatment day (t), given that they are alive and present on the colony during this day (t).

The sighting probability is calculated by considering penguins not seen during the post-treatment day (t) but seen later during the behavioural monitoring period, for example during the post-treatment day ($t+1$). Because these penguins were seen during the day ($t+1$), they had not left the colony. They were therefore present but not seen in the colony during the post-treatment day (t), allowing a sighting probability P to be calculated. Concerning survival probability, a bird seen in the colony during the day (t) would be scored as staying on the colony from this post-treatment day (t) to the next ($t+1$) if (1) it was seen during the day ($t+1$), (2) it was not seen in the colony during the day ($t+1$) but was seen later during the behavioural monitoring period; more details about the probabilistic framework are given by Lebreton et al. (Lebreton et al., 1992).

Because time since treatment could have an effect on kidnapping behaviour, we tested the likelihood of a model allowing differences in kidnapping probability between the first day of behavioural monitoring and the six following days. Moreover, to check for an effect of bromocriptine treatment on the first day of behavioural monitoring, we compared the likelihood of two nested models: (1) a model with an effect of treatment, (2) a model with no effect of treatment on the transition probability from the non-kidnapping to the kidnapping state during the first day of behavioural monitoring. To test for an effect of initial PRL level (individual covariate) on probabilities of transition, we used a logit link function: $\text{logit}(\Psi)=A+B(\text{covariate})$, where A was the intercept and B the slope. The logit link function permits constraint of a parameter (i.e. probability of transition) to be a function of a covariate (i.e. initial PRL level) by linking it to a linear formula (Lebreton et al., 1992). Moreover, the logit link function has the advantage of keeping estimates of

probabilities within the interval (0,1). The model selection was performed following the parsimony principle (Burnham and Anderson, 1998), based on Akaike's information criterion corrected for small sample size (AICc). This measure combines the goodness-of-fit of a model to data and the number of estimated model parameters and therefore reflects model parsimony (Burnham and Anderson, 1998). We started our model selection from the most general model with an effect of treatment and behavioural state on survival (S), sighting (P) probabilities and an effect of treatment on transition probabilities (Ψ) from one behavioural state to another, and subsequent models were constrained in a step-down approach (Lebreton et al., 1992). Differences between AICc values for two different nested models can be used to determine which provides the most adequate description of the data based on the fewest model parameters ($\Delta\text{AICc} = \text{AICc of the starting model} - \text{AICc of the constrained model}$). The model with the lowest AICc was considered the best fit that describes the relationship. ΔAICc values >2 are a good indicator that the constrained model is preferable. ΔAICc values <2 and >-2 indicate that models are fairly similar in their ability to describe the data, and the simplest model including the fewest model parameters was then selected by following the parsimony principle (Burnham and Anderson, 1998). ΔAICc values <-2 indicate that the starting model is preferable. We tested whether the global model provided an adequate description of our data, using the goodness-of-fit (GOF) test for multistate models implemented in U-CARE software [R. Choquet, A. M. Reboulet, R. Pradel, O. Gimenez and J. D. Lebreton (2003); *U-Care User's Guide, Version 2.0*. Mimeographed document, CEFE/CNRS, Montpellier (<ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/>)].

Results

Effect of bromocriptine on prolactin level

Both treated birds kept in captivity had similar PRL levels before the treatment (control: 24.1 ng ml^{-1} , bromocriptine: 22 ng ml^{-1}), but the bird injected with bromocriptine had lower PRL level than the control bird 3 days (control, 24.5 ng ml^{-1} ; bromocriptine, 11.9 ng ml^{-1}) and 8 days (control, 20.5 ng ml^{-1} ; bromocriptine, 6.6 ng ml^{-1}) after the injection.

Kidnapping behaviour and model selection

A total of 28 chick kidnappings were observed during the behavioural monitoring. 30.4% of the penguins treated with bromocriptine and 54.2% of the penguins treated with vehicle were sighted at least once with a chick. At capture both groups were almost identical in body mass (bromocriptine, $27.53 \pm 0.38 \text{ kg}$; control, $27.08 \pm 0.72 \text{ kg}$; t -test: $t=0.6$, $P=0.55$), sex ratio ($\chi^2=0.1$, d.f.=1, $P=0.95$), date of treatment (bromocriptine: 260.71 ± 0.73 Julian days; control: 261.52 ± 0.84 Julian days; Mann-Whitney test: $U=308$, $P=0.47$) and PRL levels (bromocriptine: $27.66 \pm 1.73 \text{ ng ml}^{-1}$; control: $26.36 \pm 1.50 \text{ ng ml}^{-1}$; $t=0.65$, $P=0.52$).

The overall GOF test revealed that the global model fitted

the data satisfactorily ($\chi^2=8.81$, d.f.=11, $P=0.64$). Starting with the general model (Fig. 2, model 1; model with an effect of treatment and behavioural state on survival (S) and sighting (P) probabilities and an effect of treatment on transition probabilities (Ψ) from one behavioural state to another), we found that survival probability did not depend on treatment (Fig. 2, models 1 and 2, $\Delta\text{AICc}=4.72$). There was also no effect of behavioural state (kidnapping or not kidnapping) on survival probability (Fig. 2, models 2 and 3, $\Delta\text{AICc}=1.80$). Sighting probability did not depend on treatment (Fig. 2, models 3 and 4, $\Delta\text{AICc}=2.12$), but on behavioural state (Fig. 2, models 4 and 5, $\Delta\text{AICc}=-6.40$). Although there was no effect of treatment on the transition probability from the kidnapping state to the non-kidnapping state (Fig. 2, models 4 and 6, $\Delta\text{AICc}=3.77$), our model selection demonstrated a strong effect of treatment on transition probability from the non-kidnapping state to the kidnapping state (Fig. 2, models 6 and 7, $\Delta\text{AICc}=-12.70$). There was no effect of time since treatment on transition probabilities for the control group (Fig. 2, models 6 and 8, $\Delta\text{AICc}=0.20$) and for the bromocriptine group (Fig. 2, models 6 and 9, $\Delta\text{AICc}=-0.94$). Moreover, the model allowing an effect of treatment on the transition probability from the non-kidnapping state to the kidnapping state during the first day of behavioural monitoring had a lower AICc than the simpler model (Fig. 2, models A and B, $\Delta\text{AICc}=-7.57$). We also observed no effect of plasma PRL levels measured prior to the injection of bromocriptine or vehicle on this transition probability for the control group (Fig. 2, models 6 and 10,

Fig. 2. Description of number of parameters (K) and AICc for various models testing for an effect of bromocriptine treatment on kidnapping behaviour in emperor penguins. Model 1 is the general starting model, with an effect of treatment and behavioural state on survival and sighting probabilities and an effect of treatment on transition probabilities. Model selection: an arrow starting from a model indicate the application of a constraint to this model. This constraint is detailed above the constrained model, which is at the end of the arrow. ΔAICc values were used to determine which model provides the best description of the data based on the fewest parameters ($\Delta\text{AICc} = \text{AICc of the starting model} - \text{AICc of the constrained model}$). ΔAICc values >2 indicate that the constrained model is preferable. ΔAICc values <2 and >-2 indicate that models are fairly similar and the model including the fewest parameters was selected. ΔAICc values <-2 indicate that the starting model is preferable. Filled and broken arrows indicate, respectively, that the constraint was selected or not. Each model was defined using the following notations: S , survival probability; P , sighting probability; Ψ^{ab} transition probability from state a to b ; 1, non-kidnapping state; 2, kidnapping state; $\Psi^{12\text{br}}/\Psi^{12\text{co}}$, Ψ^{12} within the bromocriptine/control group; treatment/state: effect of treatment/behavioural state on a given parameter; prl: effect of initial level of PRL on a given parameter; $\Psi^{12}_{\text{first}}\Psi^{12}_{2-7}$, effect of time since treatment on Ψ^{12} , which can vary between the first day and the last days of the study period. In models testing for an effect of PRL levels or time since treatment on Ψ^{12} within one group (bromocriptine/control), $\Psi^{12}_{\text{treatment}}$ was dissociated and we used this notation $\Psi^{12\text{br}}\Psi^{12\text{co}}$. Models A and B are two nested models allowing us to test an effect of treatment on kidnapping behaviour during the first day of behavioural monitoring.

$\Delta AICc = -0.34$). This effect was, however, strong in the bromocriptine group (Fig. 2, model 6 and 11, $\Delta AICc = 5.88$).

Parameter estimates indicated that the transition probability from the non-kidnapping to the kidnapping state was higher in

the control than in the bromocriptine group (Fig. 3). This difference was selected because the model with no effect of treatment on this transition probability had a much higher AICc than the model with an effect of treatment (Fig. 2, models 6

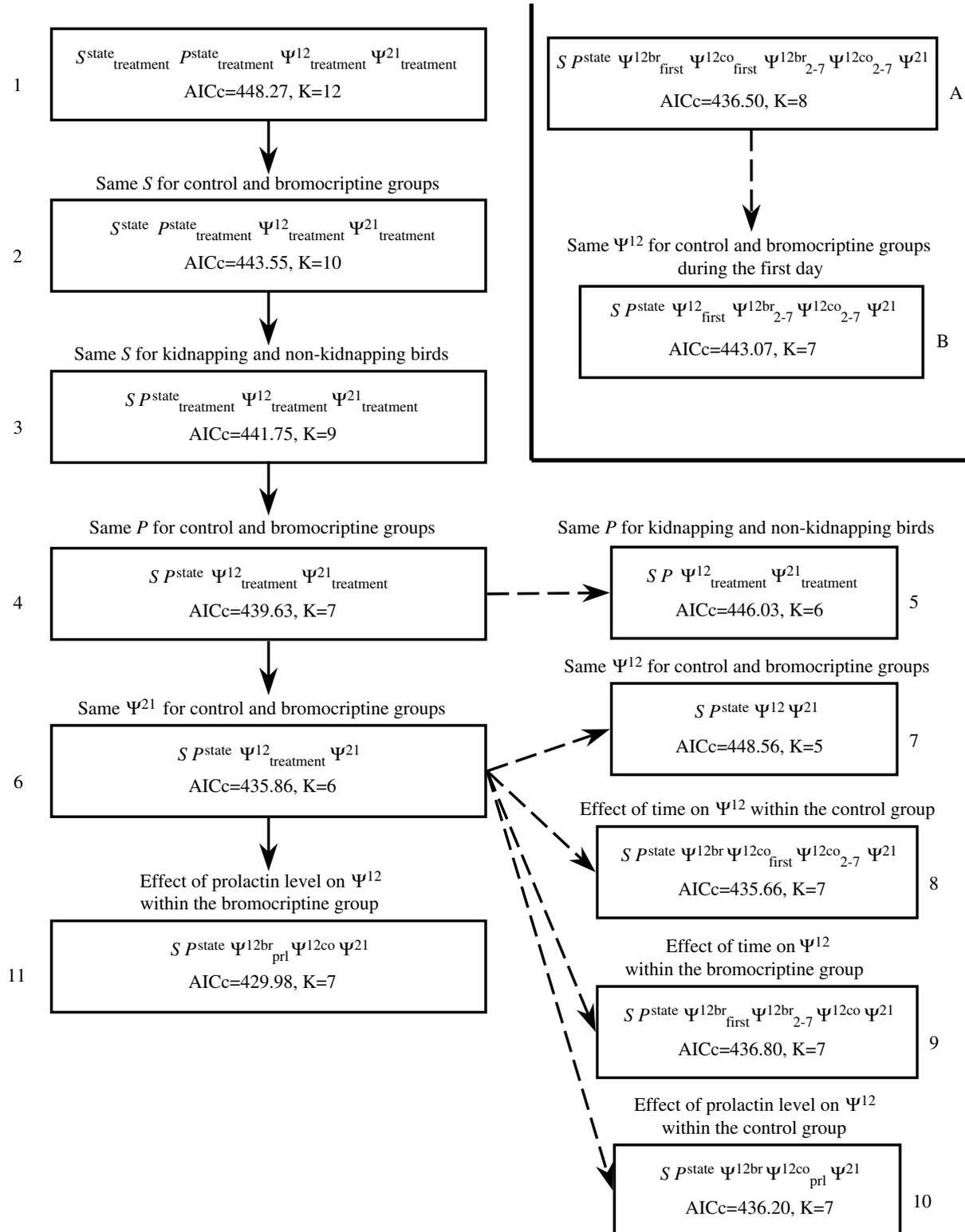


Fig. 2. See previous page for legend.

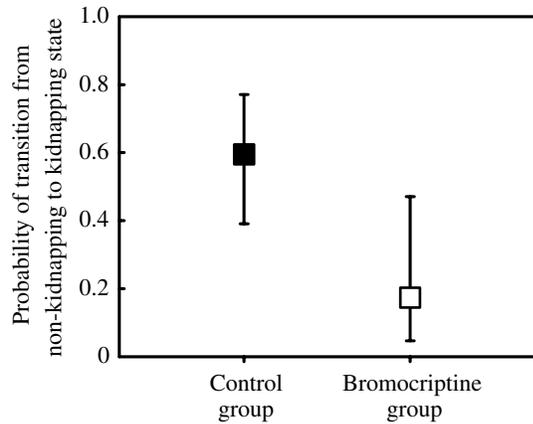


Fig. 3. Estimates of the transition probability from the non-kidnapping to the kidnapping state for prolactin inhibited (bromocriptine, $N=23$) and control individuals ($N=24$), showing 95% confidence limits. Estimates were obtained from model 11 (Fig. 2).

and 7, $\Delta\text{AICc}=-12.70$). Within the bromocriptine group, kidnapping behaviour was not totally suppressed and the transition probability from the non-kidnapping to the kidnapping state (Ψ^{12}) was positively correlated to the plasma PRL level measured before injection of bromocriptine [$\text{logit}(\Psi^{12})=A+B(\text{PRL level before injection})$, $B=1.42\pm 0.64$ (mean \pm s.e.m.), [0.16, 2.68] 95% CI]. Similarly, this relationship was selected because the model with an effect of plasma PRL level measured before injection on this transition probability within the bromocriptine group had a lower AICc than the model without this effect (Fig. 2, models 6 and 11, $\Delta\text{AICc}=5.88$). Within the bromocriptine group, kidnapers had higher PRL levels prior to the bromocriptine treatment than non-kidnapers (t -test: $t=-3.45$, $P=0.005$, Fig. 4) whereas this was not observed in the control group (t -test: $t=-0.99$, $P=0.33$).

Discussion

In this experiment, penguins treated with bromocriptine kidnapped chicks less often. Although statistics cannot be run to test for a difference in the decrease in PRL levels between bromocriptine and control groups as only one animal was kept in captivity and involved in each treatment, we are confident that the treatment decreased PRL levels, as bromocriptine administration is known to suppress PRL levels in birds (Reddy et al., 2002). Moreover, bromocriptine is particularly well known as a suppressant of PRL secretion in penguins. Jouventin and Mauget injected 30 king penguins *Aptenodytes patagonicus* with the same bromocriptine dose as in the present study, resulting in a 78% decrease in PRL levels (Jouventin and Mauget, 1996). King penguins and emperor penguins have the same endogenous mode of secretion of PRL (Garcia et al., 1996; Lormée et al., 1999) and the decrease observed in king penguins was similar to the decrease that we observed in our bromocriptine treated penguin (i.e. 75%), which confirms the efficiency of bromocriptine treatment in our study.

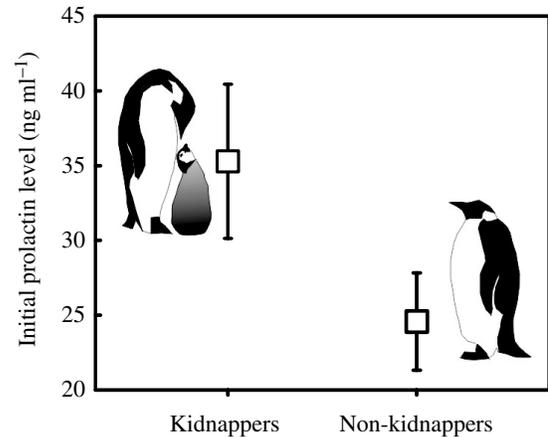


Fig. 4. Prolactin levels prior to the bromocriptine treatment for kidnapers ($N=7$) and non-kidnapers ($N=16$) within the bromocriptine group (mean \pm 95% confidence limit).

When penguins were injected with bromocriptine, the probability that they kidnapped a chick was on average 4.5 times lower than that of penguins injected with a vehicle. Although bromocriptine, as a dopamine agonist, might have reduced the probability of kidnapping by other mechanisms than its prolactin-inhibiting properties (Ben-Jonathan and Hnasko, 2001), this result is consistent with the hypothesis that kidnapping of chicks by failed breeders is the result of high residual level of PRL.

Survival probability (S) did not vary with treatment or behavioural state, suggesting that the probability to leave the colony did not depend on treatment (i.e. PRL levels). Within the control group, failed breeders had a high probability of transition from the non-kidnapping to the kidnapping state (0.77 ± 0.10). This result illustrates the high frequency of kidnapping in emperor penguins. Our results suggest that this behaviour is probably more common than previously thought in the emperor penguins; Jouventin et al. had found that only 28.7% of penguins kidnapped during the rearing period (Jouventin et al., 1995).

Although kidnapping behaviour was reduced by an injection of bromocriptine, it was not totally suppressed. This could be due to a temporary absence of effect of bromocriptine on PRL levels. It may have taken several days before bromocriptine had its full effect on PRL levels and bromocriptine-treated penguins could have therefore been more likely to engage in the kidnapping behaviour for the first day and less likely to engage in this behaviour later. We found no effect of time since treatment on transition probabilities, however. Moreover, the probability of kidnapping was affected by treatment since the first day of behavioural monitoring. These results demonstrate that bromocriptine had an effect on kidnapping probability since the day following the treatment.

Within the bromocriptine group, the model selection showed that the probability of kidnapping a chick increased with increasing plasma PRL levels measured prior to bromocriptine

treatment. Kidnappers had higher PRL levels prior to bromocriptine treatment than non-kidnappers within this group. As these relationships were not observed within the control group, it raises the question of the physiological mechanism linking PRL and kidnapping behaviour. Our results suggest that kidnapping behaviour might depend on a threshold level of PRL. Bromocriptine administration could have failed to diminish the PRL level below this threshold in penguins with the highest PRL levels prior to the treatment, which could explain why these birds still kidnapped chicks during the study whereas birds with low PRL levels prior to bromocriptine treatment did not. As a consequence, high PRL level would be necessary to promote kidnapping behaviour. Future studies should now determine what PRL level represents a threshold for kidnapping to occur by sampling blood from bromocriptine-treated penguins at the exact time they are engaged in kidnapping behaviour.

Although PRL is involved in both parental and kidnapping behaviour (Lormée et al., 1999; this study), there are some important differences between the care provided by kidnappers and parents. Kidnappers abandon the chick after few hours, suggesting that there are differences in the mechanisms underlying the expression of care between parents and kidnappers. Emperor penguin parents are able to recognize their chick by voice and they reject all solicitation for food apart from those of their own young (Jouventin et al., 1979). Therefore, kidnappers might abandon the kidnapped chick after few hours, because they have never heard its voice before and do not recognize it. Elevated PRL levels are necessary to initiate kidnapping behaviour, but they do not seem sufficient to maintain care during a long period.

In contrast to most bird species where the loss of eggs or chicks lead PRL to return rapidly to basal levels (Buntin, 1996; Chastel and Lormée, 2002), PRL secretion in several penguin species is poorly influenced by egg or chick stimuli and stays elevated for weeks and even months after failure (Garcia et al., 1996; Lormée et al., 1999; Vleck et al., 2000). This unusual pattern of PRL secretion has been interpreted as an adaptation to maintain parental care despite long absences at sea to forage (Garcia et al., 1996; Lormée et al., 1999). During breeding, emperor penguins have to undertake long foraging trips on distant ice-free areas (Ancel et al., 1992) and female emperor penguins undergo a 2 month foraging trip just after laying, coming back at the expected time of hatching to relieve their mate (Prévost, 1961). At this time, these birds will return to the colony with elevated PRL levels and not know if their mate has lost the egg or the newly hatched chick (Lormée et al., 1999). Consequently, penguins that lose their egg or their chick during a foraging trip still maintain high residual PRL levels over a long period (Garcia et al., 1996; Lormée et al., 1999; Vleck et al., 2000). This, combined with colonial breeding and the absence of a nest and territory, probably facilitates kidnapping. Previous studies reported that failed breeders become kidnappers through some process of social stimulation (Prévost, 1961; Jouventin et al., 1995), and kidnapping behaviour often occurs when a failed breeder perceives stimuli

from a chick asking for food to its parents (Jouventin et al., 1995). It suggests that both elevated prolactin levels and environmental stimuli are necessary for the display of kidnapping behaviour.

Ultimately, kidnapping behaviour does not seem to be costly for failed breeder emperor penguins. Failed breeders probably do not support the cost of raising unrelated young since in most cases kidnapping and adoption only last for a few hours (Jouventin et al., 1995). On the other hand, the benefits of kidnapping for emperor penguins are not obvious. Kidnapped chicks are seldom fed and sometimes die during the struggle for kidnapping (Jouventin et al., 1995). Young failed breeders may benefit from being kidnappers by gaining breeding experience (Riedman, 1982; Jouventin et al., 1995; Komdeur, 1996; Clutton-Brock, 2002). This is unlikely, however, since most kidnappers are known to have already bred successfully in previous years (Jouventin et al., 1995). Kin selection hypothesis (Hamilton, 1964) is also unlikely to be supported here, as kidnapping does not seem to be directed towards selected chicks. Moreover, a recent study showed that kin selection did not promote fostering behaviour among Antarctic fur seals *Arctocephalus gazella*, which have a comparable breeding system to emperor penguins with long absences at sea and breeding occurring in densely populated colonies (Hoffman and Amos, 2005). Hence, emperor penguins would have no direct fitness interest in kidnapping chicks.

Conclusion

In cooperative species there is increasing empirical evidence that group augmentation by kidnapping increases the fitness of group members (Clutton-Brock, 2002). In contrast, our experimental study suggests that kidnapping in the non-cooperative breeding emperor penguin may be due to the hormonal byproduct of a reproductive adaptation to extreme conditions, such as long foraging trips during the Antarctic winter. As kidnapping in emperor penguins offers no obvious benefits and does not seem to entail significant costs, this behaviour might be considered as neutral, and not subject to selection pressures.

This study was supported financially by the Institut Français pour la Recherche et la Technologie Polaire (IPEV Programme 109). F. Angelier was supported by a grant from CNRS/Région Poitou-Charentes. We thank H. Hoppeler, A. Lendvai and two anonymous reviewers for helpful comments on a previous version of the manuscript. At the Centre d'Etudes Biologiques de Chizé, we thank S. Dano, A. Lacroix and C. Trouvé for their excellent technical assistance with the prolactin assay.

References

- Ancel, A., Kooyman, G. L., Ponganis, P. J., Gendner, J., Lignon, J., Mestre, X., Huin, N., Thorson, P. H., Robisson, P. and Le Maho, Y. (1992). Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature* **360**, 336-339.

- Ben-Jonathan, N. and Hnasko, R.** (2001). Dopamine as a prolactin inhibitor. *Endocr. Rev.* **22**, 724-763.
- Birkhead, T. R. and Nettleship, D. N.** (1984). Alloparental care in the common murre (*Uria aalge*). *Can. J. Zool.* **62**, 2121-2124.
- Bridges, R. S. and Ronsheim, P. M.** (1990). Prolactin (PRL) regulation of maternal behavior in rats: bromocriptine treatment delays and PRL promotes the rapid onset of behavior. *Endocrinology* **126**, 837-848.
- Brown, J. L. and Vleck, C. M.** (1998). Prolactin and helping in birds: has natural selection strengthened helping behavior? *Behav. Ecol.* **9**, 541-545.
- Buntin, J. D.** (1996). Neural and hormonal control of parental behavior in birds. *Adv. Stud. Behav.* **25**, 161-213.
- Burnham, K. P. and Anderson, D. R.** (1998). *Model Selection and Inference: A Practical Information-Theoretic Approach*. New York: Springer Verlag.
- Bustamente, J. and Hiraldo, F.** (1990). Adoptions of fledglings by black and red kites. *Anim. Behav.* **39**, 804-806.
- Chastel, O. and Lormée, H.** (2002). Patterns of prolactin secretion in relation to incubation failure in a tropical seabird, the red-footed booby. *Condor* **104**, 873-876.
- Clutton-Brock, T.** (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69-72.
- Garcia, V., Jouventin, P. and Mauget, R.** (1996). Parental care and the prolactin secretion in the king penguin: an endogenously timed mechanism? *Horm. Behav.* **30**, 259-265.
- Hamilton, W. D.** (1964). The genetical evolution of social behaviour, I and II. *J. Theor. Biol.* **7**, 1-52.
- Heinsohn, R. G.** (1991). Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Anim. Behav.* **41**, 1097-1100.
- Heinsohn, R. G. and Legge, S.** (1999). The cost of helping. *Trends Ecol. Evol.* **14**, 53-57.
- Hoffman, J. I. and Amos, W.** (2005). Does kin selection influence fostering behaviour in Antarctic fur seals (*Arctocephalus gazella*). *Proc. R. Soc. Lond. B* **272**, 2017-2022.
- Jouventin, P. and Mauget, R.** (1996). The endocrine basis of the reproductive cycle in the king penguin (*Aptenodytes patagonicus*). *J. Zool. Lond.* **238**, 665-678.
- Jouventin, P., Guillotin, M. and Cornet, A.** (1979). Le chant du manchot empereur et sa signification adaptative. *Behaviour* **70**, 231-250.
- Jouventin, P., Barbraud, C. and Rubin, M.** (1995). Adoption in the emperor penguin. *Anim. Behav.* **50**, 1023-1029.
- Khan, M. Z., McNabb, F. M. A., Walters, J. R. and Sharp, P. J.** (2001). Patterns of testosterone and prolactin concentrations and reproductive behaviour of helpers and breeders in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*). *Horm. Behav.* **40**, 1-13.
- Komdeur, J.** (1996). Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* **7**, 326-333.
- Lebreton, J. D., Burnham, K. P., Clobert, J. and Anderson, D. R.** (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67-118.
- Lormée, H., Jouventin, P., Chastel, O. and Mauget, R.** (1999). Endocrine correlates of parental care in an Antarctic winter breeding seabird, the emperor penguin, *Aptenodytes forsteri*. *Horm. Behav.* **35**, 9-17.
- Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L. and Link, W. A.** (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology* **75**, 2052-2065.
- Prévost, J.** (1961). *Ecologie du Manchot Empereur*. Paris: Hermann.
- Reddy, I. J., David, C. G., Sarma, P. V. and Singh, K.** (2002). The possible role of prolactin in laying performance and steroid hormone secretion in domestic hen (*Gallus domesticus*). *Gen. Comp. Endocrinol.* **127**, 249-255.
- Riedman, M. L.** (1982). The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.* **57**, 405-435.
- Roberts, R. L., Jenkins, K. T., Lawler, T., Wegner, F. H. and Newman, J. D.** (2001). Bromocriptine administration lowers serum prolactin and disrupts parental responsiveness in common marmosets (*Callithrix j. jacchus*). *Horm. Behav.* **39**, 106-112.
- Schoech, S. J., Mumme, R. L. and Wingfield, J. C.** (1996). Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens*. *Anim. Behav.* **52**, 445-456.
- Stearns, S. C.** (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Vleck, C. M., Mays, N. A., Dawson, J. W. and Goldsmith, A. R.** (1991). Hormonal correlates of parental and helping behavior in cooperatively breeding Harris' hawks (*Parabuteo unicinctus*). *Auk* **108**, 638-648.
- Vleck, C. M., Ross, L. L., Vleck, D. and Bucher, T. L.** (2000). Prolactin and parental behavior in Adélie penguins: effect of absence from nest, incubation length, and nest failure. *Horm. Behav.* **38**, 149-158.
- White, G. C. and Burnham, K. P.** (1999). Program MARK: survival rate estimation from both live and dead encounters. *Bird Study* **46**, S120-S139.
- Wilson, E. O.** (1975). *Sociobiology: The New Synthesis*. Cambridge, MA: Belknap Press of Harvard University Press.