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

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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 kidnappers 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 kidnappers 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 kidnappers 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 kidnappers 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,

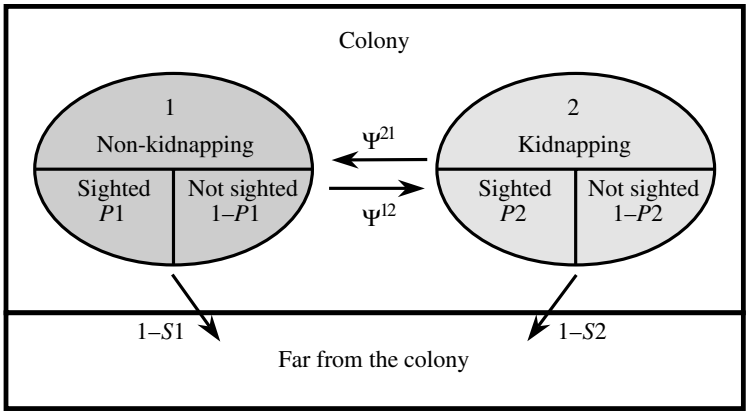

Fig. 1. Modelling kidnapping behaviour with a multi-state approach in the emperor penguin. States 1 and 2 are, respectively, the non-kidnapping state and the kidnapping state. Ψ^{ab} is the transition probability from state a to state b over one post treatment day (t) to the next one (t+1). Ψ^{12} is 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: logit(Ψ)=A+B(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 (ΔAICc=AICc of the starting model – 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±0.38 kg; control, 27.08±0.72 kg; *t*-test: t=0.6, P=0.55), sex ratio (χ^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±1.73 ng ml^{-1}; control: 26.36±1.50 ng ml^{-1}; t=0.65, P=0.52).

The overall GOF test revealed that the global model fitted the data satisfactorily (χ^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, ΔAICc=4.72). There was also no effect of behavioural state (kidnapping or not kidnapping) on survival probability (Fig. 2, models 2 and 3, ΔAICc=1.80). Sighting probability did not depend on treatment (Fig. 2, models 3 and 4, ΔAICc=2.12), but on behavioural state (Fig. 2, models 4 and 5, ΔAICc=–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, ΔAICc=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, ΔAICc=–12.70). There was no effect of time since treatment on transition probabilities for the control group (Fig. 2, models 6 and 8, ΔAICc=0.20) and for the bromocriptine group (Fig. 2, models 6 and 9, ΔAICc=–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, ΔAICc=–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 (ΔAICc=AICc of the starting model–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; Ψ^{12br}/Ψ^{12co}, 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; $\Psi^{12}{}_{first}\Psi^{12}{}_{2\text{-}7}$, 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), $\Psi^{12}{}_{treatment}$ was dissociated and we used this notation Ψ^{12br} Ψ^{12co}. 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.

ΔAICc=–0.34). This effect was, however, strong in the bromocriptine group (Fig. 2, model 6 and 11, ΔAICc=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

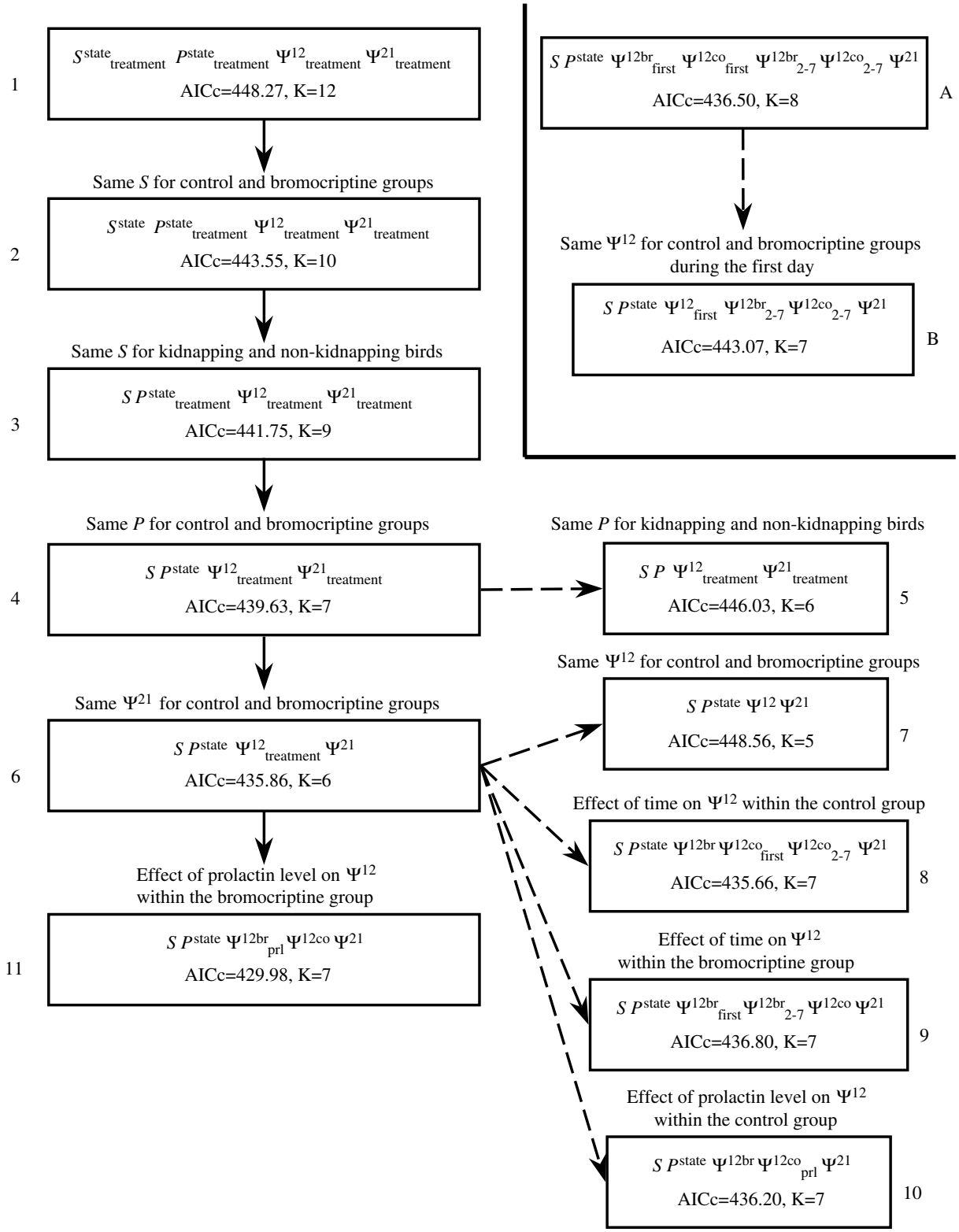

Fig. 2. See previous page for legend.

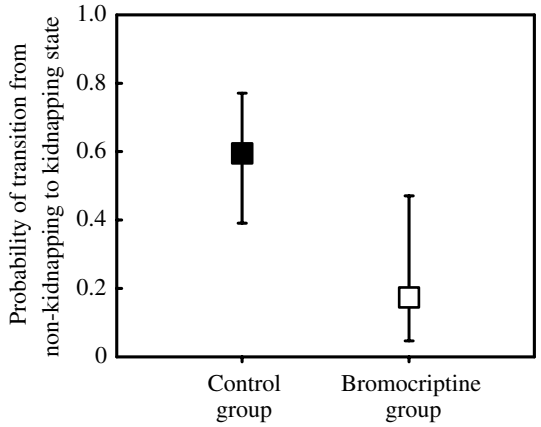

Fig. 3. Estimates of the transition probability from the non-kidnapping to the kidnapping state for prolactin inhibited (bromocriptine, *N*=23) and control individuals (*N*=24), showing 95% confidence limits. Estimates were obtained from model 11 (Fig. 2).

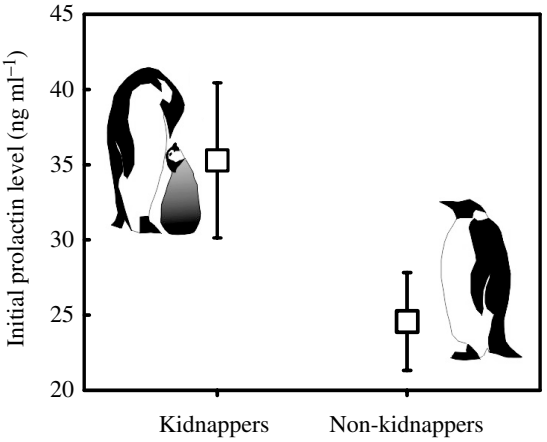

Fig. 4. Prolactin levels prior to the bromocriptine treatment for kidnappers (*N*=7) and non-kidnappers (*N*=16) within the bromocriptine group (mean ± 95% confidence limit).

and 7, ΔAICc=–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 [logit (Ψ^{12})=A+B(PRL level before injection), B=1.42±0.64 (mean ± 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, ΔAICc=5.88). Within the bromocriptine group, kidnappers had higher PRL levels prior to the bromocriptine treatment than non-kidnappers (*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.

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 that 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.

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Inside JEB

EMBRYOS SENSE SEISMIC EVENTS

Karen Warkentin knew she'd have some interesting questions to answer when she saw a hungry snake attacking a clutch of near-term red-eyed treefrog eggs in the lab. As the predator started tucking in to the eggs, tiny frog embryos began tumbling from the clutch, even though they should have waited another 2 days before hatching. Warkentin eventually discovered that the tadpoles were making a tough decision: to escape the snake by fleeing to the water, even though they are much more vulnerable to aquatic predators at such an early age. Intrigued by the youngster's decision, Warkentin was curious to find out which cues had triggered their evacuation. Warkentin began to suspect that vibrations, generated by the snake's assault, prompted the treefrog's bid for freedom, but why didn't other less sinister vibrations send the youngsters tumbling free too? Curious to know how the embryos distinguished a life-threatening attack from vibrations caused by rain or rustling leaves, Warkentin and her student Michael Caldwell decided to see what makes vibration sequences scary for red-eyed treefrog embryos (p. 1376).

Travelling to the Smithsonian Tropical Research Institute at Gamboa, Panama, Warkentin and Caldwell collected frogspawn from trees growing over a local pond. Back in the lab, the team waited until the eggs were 5 days old before attaching a vibrating probe to the clutch to shake the embryos up. Teaming up with Gregory McDaniel, a vibrations engineer, Warkentin designed 32 white noise vibration patterns, with bursts of vibration ranging from 0.5–20 s interspersed with gaps ranging from 0.5–100 s. Exposing egg clutches to the vibrations, the team recorded how many embryos were scared enough to hatch during the following 10 minutes.

Analysing the embryo's escapology, Warkentin realised that the frogs weren't responding to the percentage of time filled with vibration or the length of the time cycle that the pattern repeated over. However, the vibration duration and gap between vibration bursts had a profound effect on the embryo's desire to hatch; 0.5 s bursts combined with 1.5-2.5 s gaps were very scary, with three quarters of the embryos deciding to take their chances in the water, but combining a scary 0.5 s burst with a lengthy gap wasn't at all scary. 'Vibration duration and interval appear to function as two necessary elements of a composite cue' says Warkentin. The team also realised that the embryos sometimes waited for up to a minute after the vibrations started before beginning to hatch. Warkentin explains that the treefrog eggs are secured with jelly and so are quite tough for the snake to tear loose, giving the embryos enough time to sample several vibration cycles before making their life or death decision.

So how do the embryos sense these seismic events? Warkentin isn't sure. She explains that it is possible that the embryo's lateral line neuromasts pick up the vibrations, or that the embryos simply sense the signal by sloshing around within their capsules. But that is one of the unresolved questions that will keep her returning to Panama for years to come.

10.1242/jeb.02216

Warkentin, K. M., Caldwell, M. S. and McDaniel, J. G. (2006). Temporal pattern cues in vibrational risk assessment by embryos of the red-eyed treefrog, *Agalychnis callidryas*. *J. Exp. Biol.* **209**, 1376-1384.

STICKY WEBS SUFFER FROM STARVATION

Spiders are a byword for industry. These diligent little engineers constantly tear down their webs and rebuild them in an effort to snare a snack. However, despite their ingenuity some spiders go hungry for days while waiting, so what effect does starvation have on a web's composition? Mark Townley explains that although a web's structure is largely derived from silk, 40-70% of an orb-web's mass is composed of the low-molecular-mass compounds (LMM) that contribute to the web's adhesive coating. Edward Tillinghast and Townley decided to analyse the LMM

components in orb-web glue to find out which glue compounds the spiders synthesize from scratch and what happens to the adhesive when spiders go without (p. 1463).

Knowing that labelled carbon from radioactive glucose would be incorporated in LMM compounds that the spiders synthesized, Townley offered two species of *Argiope* spiders a sip of radioactive glucose solution before collecting their webs to find out which LMMs were home made and which supplied by the diet. Having washed the adhesive from the webs, Townley isolated individual LMM components by electrophoresis before identifying them with NMR and found that the spiders were producing radioactive GABamide, glycine and alanine; the spiders were synthesising these compounds. But choline and glycine betaine remained unaffected by the arachnid's hot glucose drink; the spiders derived these compounds directly from their diet.

Keen to discover which adhesive components were most affected when the spiders went hungry, Townley and Tillinghast collected *Argiope* and *Araneus* spiders and divided them into two groups, fed and unfed, to compare the effects of starvation on the web's adhesive composition. But spider physiology seemed intent on confounding Townley's analysis. Townley explains that the fed spiders continued with normal physiological functions such as moulting and egg production, but most of these activities were severely reduced or even abolished in the starving spiders, making it tricky to isolate the effects of starvation from these routine physiological demands.

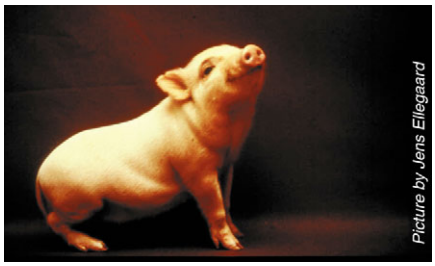
Collecting webs from both groups of spiders over the course of several weeks, Townley patiently analysed the adhesive's components from the vanishingly small samples. Teaming up with plant statistician Christopher Neefus, to identify consistent trends in the glue's changing composition, Townley found that the proportion of synthesised compounds in the adhesive, such as GABamide and glycine, increased, and the proportion of diet-derived compounds decreased, as the spiders became hungrier. And when Townley compared the fed spiders' adhesive composition with that of the starved spiders, both sets of spiders produced similar trends; the fed spiders also rapidly lost components derived from their diet while enriching the self-synthesised materials. Why was the glue composition varying in similar ways, even though half of the spiders were going hungry while the rest were well fed?

Townley suspects that several factors account for the similarity. He suggests that the fed spiders invested the surplus from their diet in activities that starved spiders avoid. One other factor also affected both groups equally; all of the spiders suffered from losing their webs. He explains that spiders constantly recycle their webs, devouring the old before constructing new ones. By taking away the resources invested in the web, Townley suspects that he was depriving the spiders of essential adhesive components that the arachnids normally recycle.

10.1242/jeb.02214

Townley, M. A., Tillinghast, E. K. and Neefus, C. D. (2006). Changes in composition of spider orb web sticky droplets with starvation and web removal, and synthesis of sticky droplet compounds. *J. Exp. Biol.* **209**, 1463-1486.

LEARNING FROM PIG BRAINS



As far as we know, the human brain is one of the most complex structures in the universe. Capable of astounding feats, our brain has fascinated us for centuries but its function has proved difficult to unravel. Given the ethical issues associated with brain research, the search has been on for the last few decades to find a brain model that could teach us about human brain development, and recent interest has focused on the pig. Jacob Jelsing explains that pig brains are similar to human brains in several respects; they have many of the same morphological features, are quite large and all of the cortical neurons appear to be fully developed at birth. But other aspects of the pig brain are less well characterised. Jelsing, working with Ralf Hemmingsen and Bente Pakkenberg, decided to characterise the pig cortex, the region of brain responsible for processing most of our conscious behaviour, by counting the number of neurons in this fundamental structure (p. 1454).

But rather than looking at just one breed of pig, the team decided to investigate two; a domestic Danish Landrace, Yorkshire crossbreed, and an experimental pig breed, the diminutive Göttingen minipig. Jelsing explains that although the domestic breed is more numerous than the minipig, the minipig's smaller stature and freedom from disruptive pathogens makes them a more attractive breed to work with from the neurobiologists perspective. Aage Olsen and Nanna Grand supplied Jelsing with brains from pigs of both species ready for the team to prepare wafer-thin brain slices before beginning the painstaking task of counting cortex neurons.

Fortunately, the team didn't have to count every single neuron in each cortical sample. Jelsing knew that if he systematically selected brain sections from randomly selected pigs he could calculate the total number of neurons in the cortex, despite having only counted a tiny fraction of the total neurons in the tissue. First Jelsing systematically chose brain slices and then Rune Nielsen counted the number of neurons in a few systematically chosen areas of each section. So long as Jelsing and Nielsen had chosen regions from all of the cortical tissue at random, but then sampled them in a systematic way, they could calculate the total number of neurones in both cortices.

After Nielsen had spent several days peering through a microscope at the delicately stained samples, the team were able to calculate the number of cortical neurons that each breed had at birth: 425 million in the domestic pig and 253 million in the smaller minipig. But when the team calculated the number of neurons in the adults' brains, they were in for a surprise; while the domestic pig's neuron count had hardly changed, the minipig's had increased significantly to 324 million. Unlike the neurons in the human cortex, which do not develop postnatally, the minipig's neurons had continued developing after birth. Jelsing does not know how long it takes the minipig's brain to complete development but it could be anything from weeks to several months. Given the shock finding that the Göttingen minipig's brain continues developing after birth, the team suggest that the domestic pig's brain may be a better model for human brain development than the smaller minipig's.

10.1242/jeb.02215

Jelsing, J., Nielsen, R., Olsen, A. K., Grand, N., Hemmingsen, R. and Pakkenberg, B. (2006). The postnatal development of neocortical neurons and glial cells in the Göttingen minipig and the domestic pig brain. *J. Exp. Biol.* **209**, 1454-1462.

PROLACTIN PROMOTES PENGUIN KIDNAPS

It's probably an emperor penguin parent's worse nightmare: having to defend their chick from a kidnapper's attack. Sadly, on the occasions when a kidnap bid has succeeded, the kidnapper often abandons their victim several hours later. But what drives the kidnapper to such a fruitless act? Frédéric Angelier and colleagues wondered whether kidnapping behaviour might be caused by unusually high levels of the parenting hormone, prolactin, in penguin parents who have lost their own chick (p. 1413).

The team injected failed penguin parents with bromocriptine to artificially reduce the birds' prolactin levels and waited to see if the incidence of kidnapping declined too. Amazingly, the probability that a failed parent would stage an abduction fell 4.5 fold when their hormone levels were reduced. Although lowering the birds' prolactin levels hadn't abolished the behaviour, it had modified it.

But why do the failed parents maintain such high levels of prolactin when prolactin levels fall in other species that have lost their chicks, especially when the hormone has such drastic consequences? Angelier and colleagues suspect that the emperor penguins sustain high levels of prolactin to encourage them to return to their chick after a lengthy separation. Sadly, this incentive to come home after a long foraging trip seems to have a nasty side effect when parents return to find their chick gone.

10.1242/jeb.02217

Angelier, F., Barbraud, C., Lormée, H., Prud'homme, F. and Chastel, O. (2006). Kidnapping of chicks in emperor penguins: a hormonal by-product? *J. Exp. Biol.* **209**, 1413-1420.

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