Endocrine Correlates of Parental Care in an Antarctic Winter Breeding Seabird, the Emperor Penguin, *Aptenodytes forsteri*

Hervé Lormée,* Pierre Jouventin,* Olivier Chastel,*
and Robert Mauget†

*Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360
Villiers en bois, France; and †Muséum National d'Histoire Naturelle, Laboratoire de
Conservation des Espèces Animales, Parc Zoologique de Paris,
53 Avenue de St. Maurice, 75012 Paris, France

Plasma levels of luteinizing hormone (LH) and prolactin associated with parental behavior were measured in the Antarctic winter breeding emperor penguin, *Aptenodytes forsteri*. Males exclusively incubate the egg while females exclusively brood the nonhomeothermic young; both sexes alternate in rearing the homeothermic young. Birds were sampled on arrival from the sea through egg laying, incubation, and brooding. All parent birds lost their chicks at the end of the brooding period due to harsh weather but sampling continued. In females, LH titers dropped after egg laying but levels were restored when the birds returned from the sea to brood the chicks and were not depressed by high prolactin levels. Plasma prolactin remained low in males captured on arrival and kept until the free-living males finished incubation. In breeders, prolactin secretion increased during the pre-laying period when day length decreased. Prolactin levels stayed elevated in males during incubation and in brooding females returning after a 2-month absence at sea. Prolactin values were higher in brooding females than in males ending incubation or returning in late brooding. These levels did not drop after chick loss, and the sexual difference in prolactin values was maintained after breeding failure. In emperor penguins, increased prolactin secretion appears to be triggered around the time of egg laying and continues, driven by an endogenous mechanism, through incubation and brooding until rearing is completed. Prolactin secretion independent of external stimuli may have evolved in pelagic seabirds to maintain parental care despite long absences at sea from the breeding colony. © 1999 Academic Press

The relationships among LH (gonadotropin hormone), prolactin (hypophyseal hormone), and the events of reproduction, from mating to the end of chick rearing, have been investigated primarily in terrestrial temperate zone avian species, among which the dominant taxa have been galliforms, columbiforms, and passeriforms (Buntin, 1996). In the most widespread pattern, although not universal for all bird species, levels of circulating LH are high during the courtship and laying period and return to basal levels as incubation starts (Ball, 1991). Simultaneous with the decline of plasma LH levels, plasma prolactin levels raise and are maintained thereafter during the whole incubation period, having a depressive effect on gonadotropin secretion (Sharp, Macnamee, Sterling, Lea, and Pedersen, 1988; Buntin, Lea, and Figge, 1988). Prolactin secretion is known to decline steadily immediately after hatching in precocial species or at the end of the brooding period in altricial species. The increase in prolactin secretion, combined with still high but declining sex steroids, seems to facilitate the transition from courtship to incubation behavior (El Halawani, Silby, Behnke, and Fehrer, 1986). In spring breeders, as first shown in the European starling *Sturnus vulgaris,* prolactin secretion is photoperiodically induced, even in nonbreeding individuals (Dawson and Goldsmith, 1985). Indeed, a large variety of environmental factors can affect plasma prolactin levels; tactile stimuli from eggs or visual stimuli from the nest, eggs, or incubating mate can stimulate prolactin secretion (Buntin, 1996). It has been experimentally shown in the Pied flycatcher, *Ficedula hypoleuca,* and the ring dove, *Streptopelia risoria,* that newly hatched chicks in the nest can maintain high levels of circulating prolactin (Silverin and Goldsmith, 1984; Lea, Vowles, and Dick, 1986).

Removal of these stimuli resulted in a decrease in plasma prolactin and the termination of parental behavior. It is worth noting that in several species, prolactin secretion slightly differs from this pattern. For example, the onset of prolactin secretion occurs a few days after the beginning of incubation in the ring dove (Lea *et al.,* 1986). In the Common sandpiper, *Actitis macularia,* and the pied flycatcher, there is no clear relationship between the decline of prolactin levels and the end of brooding behavior (Gratto-Trevor, Oring, Fivizzani, El Halawani, and Cooke, 1990; Silverin and Goldsmith, 1990). These contradictory results strongly suggest that some other factors may affect the regulation of prolactin secretion.

In pelagic seabirds, the relationship between prolactin secretion and parental behavior appears to be more complex. Pelagic seabirds exhibit extended breeding periods (up to several months) and have to commute from remote oceanic feeding areas to their breeding places. This circumstance implies long parental absences, several days to several months, from eggs or chicks (Nelson, 1980; Croxall, 1984). Previous studies conducted on Cape gannets, *Sula capensis,* and several *Diomedea* albatrosses showed no obvious relationship between stimuli from the eggs or chicks and the variation in prolactin values. Indeed, breeding adults come ashore with prolactin levels as high as those they had when they left the nest (Hall, 1986; Hector and Goldsmith, 1985). Furthermore, it has been shown in albatrosses that experimental manipulation of the incubation period failed to produce any change in the pattern of prolactin secretion. The authors confirmed "the complex relationship between prolactin and reproductive behavior" and concluded that "there was clear evidence that the hormone is not induced in a simple way by events like changing photoperiod or copulation." More recently, Garcia, Jouventin, and Mauget (1996) studied the hormonal pattern underlying King penguin, *Aptenodytes patagonicus,* reproductive behavior. In this species the reproductive cycle lasts 14 months; adults interrupt provisioning for the chick during winter, stay at sea for 4 months, and then coming back the following spring to rear the chick (Weimerskich, Stahl, and Jouventin, 1992). The former authors have pointed out that prolactin secretion was maintained regardless of stimuli from egg or chick and suggested that prolactin secretion could be endogenously timed, i.e., induced by the changes in endocrinological status after copulation and thereafter maintained for a fixed time. They hypothesized that such a prolactin pattern might be present in other pelagic seabirds.

Emperor penguins, *Aptenodytes forsteri,* are extreme in many aspects of their morphology, physiology, behavior, and ecology. They are the only birds that breed truly in winter on sea ice around the Antarctic continent, where they cope with the harshest conditions faced by any bird. Emperor penguins arrive on their breeding grounds in late autumn (March–April; Fig. 1) and females lay in May, when sea ice is very extensive. After laying, females immediately return to the sea, leaving the males to carry out the entire incubation in a single shift (64 days on average). Females come back only in July during the hatching period to relieve the fasting male and to feed and brood the newborn chick. The nonhomeothermic chick is brooded by the female for a 3-week period until late August. Males return at this time, when the chick is nearly homeothermic. Both parents alternate chick-feeding visits and foraging trips at sea until early December (see Fig. 1; Prévost, 1961; Isenmann and Jouventin, 1970; Jouventin, 1971). With the emperor penguin we have the opportunity to explore LH and prolactin profiles associated with an unusual breeding pattern.

In this paper, we focus on the endocrine basis of parental behavior in Emperor penguins, taking LH and prolactin into consideration. We describe LH and prolactin secretion throughout breeding (from arrival to brooding) and check particularly for consistency of the results with an endogenous regulation of prolactin secretion. Finally, we pay attention to differences in prolactin levels between the sexes to verify if the prolactin values of each sex closely reflect its implication in parental duties.

METHODS

Study Area and Field Methods

This study was carried out at Pointe Géologie Archipelago (66°40′ S, 140°01′ E), Adélie land, Antarctica, during the 1994 and 1996 breeding seasons (around 3300 pairs). Birds were identified using rings or dyeing with picric acid marks on the belly and were sexed using vocal dimorphism (males have fewer syllables per song than females; Jouventin, Guillotin, and Cornet, 1979). In July 1994, breeding males ($N = 18$) were blood sampled as they were leaving the colony at the end of the incubation period (Fig. 1). At the same time, 14 breeding females were blood sampled as they were returning from the sea to relieve their mates (Fig. 1). In August 1994, 6 males were blood sampled when they returned from the sea before the brooding period
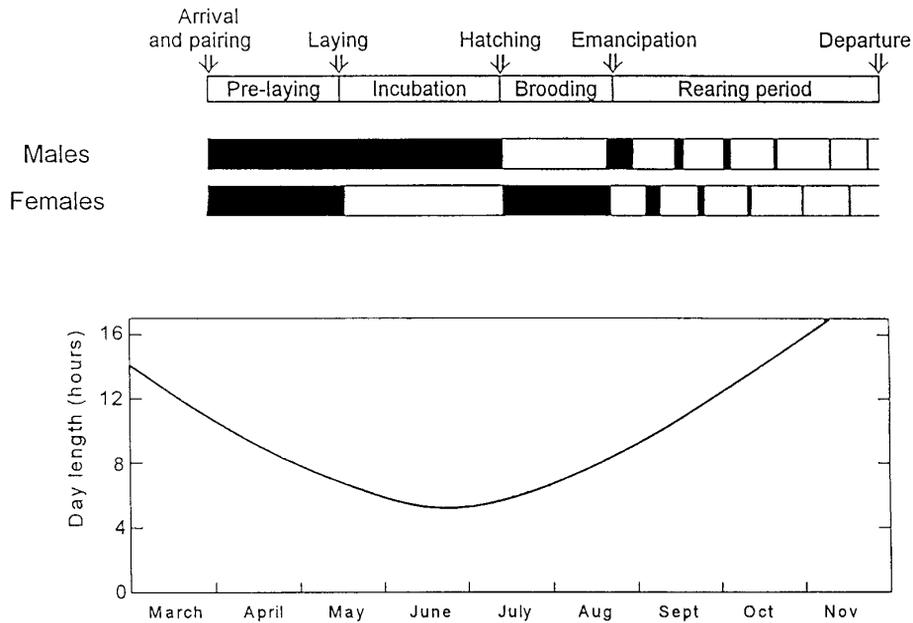
FIG. 1. Breeding phenology of the emperor penguin. Presence (■) and absence (□) of breeding birds (from Jouventin, Barbraud, and Rubin, 1995). Variation in day length is shown below.

ended (Fig. 1). Because of a severe winter, a massive breeding failure occurred during late brooding stage (less than 1% of total fledging success); as a result, all marked or ringed breeding birds lost their chicks during this period. These failed breeders were blood sampled later in the season (Fig. 4; September: 7 males, 5 females; November: 5 males, 5 females). In 1996, birds were blood sampled as they were arriving at the colony (arrival, Fig. 1; 9 males, 1 female) and during the prelaying period (7 males, 5 females). Twelve females leaving the colony after laying were also sampled. Additionally, blood samples collected in 1992 were kindly provided by Dr. Groscolas (CEPE/CNRS, Strasbourg). These blood samples were collected from arriving males, before mating. To study variations in prolactin concentration in nonbreeders, 4 of these birds were kept in captivity for 4 months (the period corresponding in males to arrival until the end of incubation). During this time, just as males in the colony did, they fasted until early July when they were sampled again and released.

Blood Sampling

Birds were blood sampled immediately after capture when they were at the edge of the colony, to prevent disturbances. Five milliliters of blood (range 0.5–5 ml) was collected between 0900 and 1500 from the marginal vein of the flipper into heparinized tubes and immediately centrifuged. The plasmas were stored at −20°C until they were assayed in France. Incubating males were not sampled to avoid disturbance. Male emperor penguins incubate on their feet and any attempt to catch and handle these birds definitively leads to egg desertion.

Hormone Assays

Following the methods previously described for king penguin plasma (Cherel, Mauget, Lacroix, and Gilles, 1994; Mauget, Jouventin, Lacroix, and Ishii, 1994), prolactin and LH radioimmunoassays were conducted and validated for emperor penguin plasma. Pooled plasma samples of emperor penguins produced dose–response curves that paralleled the chicken prolactin and LH standard curves (Fig. 2); their slopes were not significantly different (−1.18 and −1.55, respectively, for prolactin; −2.25 and −2.24, respectively, for LH). The intra-assay coefficients of variation for LH and prolactin were 4.8 and 2.4%, respectively. The interassay coefficient of variation for
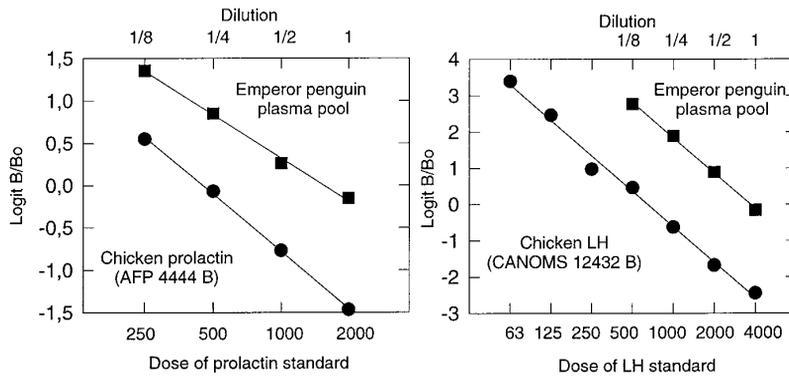
FIG. 2. Dose–response curves of chicken prolactin and LH and emperor penguin plasma. Prolactin and LH standards are expressed in pg/tube.

prolactin was 14.17%. Only two assays were performed for LH, with a variation of 14.1%.

Statistical Analysis

Because values for plasma concentration of LH and prolactin were not normally distributed, we used non-parametric Kruskal–Wallis, Mann–Whitney U tests, or Wilcoxon's rank sum z tests. All mean hormone concentrations are given ± standard error.

RESULTS

LH Values from Arrival to Brooding

Female LH levels varied significantly across the sampling periods (Kruskal–Wallis H test, $H_2 = 16.713$, $P < 0.001$) (Fig. 3a). The one arriving female had a LH plasma level of 2.66 ng/ml. Female LH levels dropped significantly between the prelaying period and their departure to the sea (multiple comparison pairwise z test: $P < 0.05$). Females returning during the brooding period exhibited higher LH titers than those exhibited when departing to sea after laying (Fig. 3a; z test: $P < 0.01$). In males, there was no significant variation in LH values between sampling periods (H test, $H_2 = 1.913$, $P = 0.384$). During the brooding period, females tended to have higher LH plasma levels than males but the difference was not statistically significant (Mann–Whitney U test, $P > 0.05$).

Prolactin Values from Arrival to Brooding

For both sexes, prolactin levels increased significantly from the arrival period to the brooding period (males: H test, $H_3 = 25.498$, $P < 0.001$; females: H test, $H_2 = 23.68$, $P < 0.001$). The one arriving female had a prolactin level of 7.02 ng/ml (Fig. 3b). When departing after laying, female prolactin levels tended to be higher than during the prelaying period (z test, $P > 0.05$). There was a sharp increase in prolactin levels in females returning to brood despite having been absent from the colony for 2 months (z test, $P < 0.01$).

On arrival, males had low prolactin levels (Fig. 3b). Among captive birds, low prolactin values stayed unchanged from arrival until their release after a 4-month fast (Fig. 4; U test, $P > 0.05$). In contrast, prolactin levels increased in males from arrival to the prelaying period (z test, $P < 0.05$). Afterward there was no significant variation in prolactin levels (Fig. 3b; z test, $P > 0.05$). Plasma levels of circulating prolactin were significantly higher in males during the prelaying period (Fig. 4a; U test, $U = 5$, $P ≤ 0.05$). Conversely, prolactin values of brooding females were higher than those of males departing after incubation (U test, $U = 12$, $P < 0.001$) or coming back at the end of the brooding period (U test, $U = 0$, $P ≤ 0.01$).

LH Values in Failed Breeders

In males and females, LH values of birds that lost their chick during the brooding period stayed unchanged from September to November (Fig. 5a; U tests: females, $P > 0.05$; males, $P > 0.05$). There was no difference in LH titers between males and females (U test, $P > 0.05$). In males, LH values were similar to those of breeders sampled at the end of the incubation period or returning late in the brooding period (Mann–Whitney U test, $P > 0.05$). In females, LH titers of failed breeders were lower than those of brooding birds (Mann–Whitney U test, $P < 0.05$).
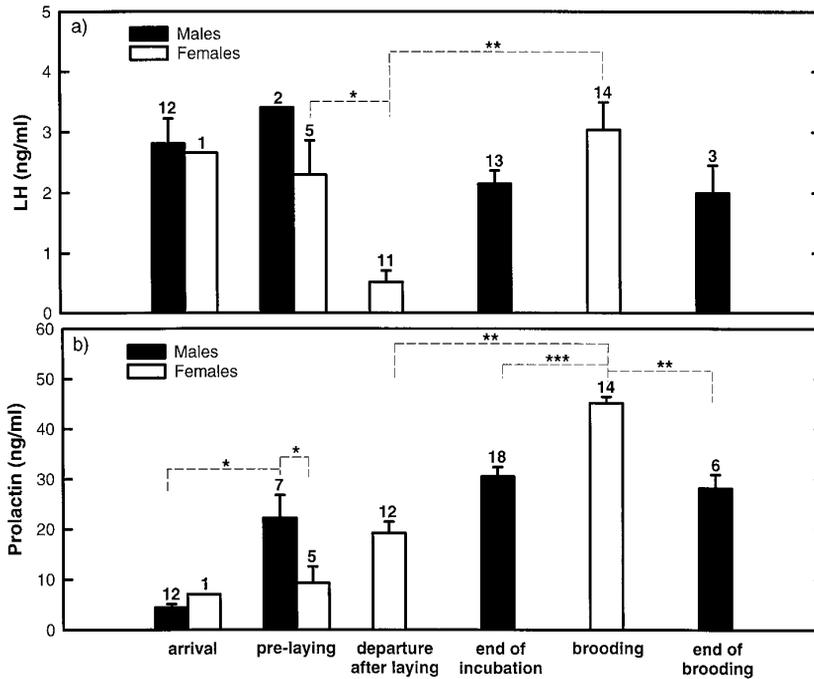
FIG. 3. a) Variation in mean plasma LH ($\pm$ SE) in breeding emperor penguins from arrival to the brooding period (* = $P < 0.05$, ** = $P < 0.01$, z test); sample sizes are given above the bars. b) Variation in mean ($\pm$ SE) plasma prolactin in breeding emperor penguins from arrival to the brooding period (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, z test and U test). Sample sizes are given above the bars.

Prolactin Values in Failed Breeders

In males and females, prolactin titers stayed unchanged from September to November (Fig. 5b; U tests: females, $P > 0.05$; males, $P > 0.05$). Prolactin titers were significantly higher in females (September and November; U test, $U = 1$, $P \leq 0.01$). In males, prolactin values of failed breeders did not significantly differ from those of males departing after the incubation period or returning at the end of the brooding period (U test, $P > 0.05$). Conversely, in females, prolactin levels of failed breeders were lower than those of brooding birds (U test, $P < 0.01$).

DISCUSSION

Variation of LH Levels

In birds, LH levels are typically elevated during laying in both sexes and decline as incubation begins (Johnson, 1986). In the emperor penguin, plasma LH levels remained above 2 ng/ml from arrival to the end of brooding and thus appeared not to be depressed by increasing

plasma prolactin levels as in previously studied species (Bantam hen, *Gallus domesticus:* Sharp, Scanes, Williams, Harvey, and Chadwick, 1979; gentoo penguin, *Pygoscelis papua:* Mauget, Garcia, and Jouventin, 1995). In females, LH levels temporarily dropped after laying but initial levels were restored when the females returned to brood the chicks. The tendency, although not significant, for females to exhibit higher LH values than males during the brooding period is in agreement with the first findings of Groscolas, Jallageas, Goldsmith, and Assenmacher (1986) on the same species. They suggested that the maintenance of high LH values in female emperor penguins might be related to brooding behavior. This possible link between brooding behavior and elevated LH values in female emperor penguins is supported by our observation that LH levels decreased significantly in females that lost their chicks and by the low LH levels measured by Groscolas *et al.* (1986) in females rearing homeothermic chicks. Female emperor penguins assume the majority of the brooding activities (for 3 weeks) at the time when the risks of chick kidnapping by failed breeders are increasing (Jouventin, Barbraud, and Rubin, 1995). Hence, brooding behavior also includes the de-
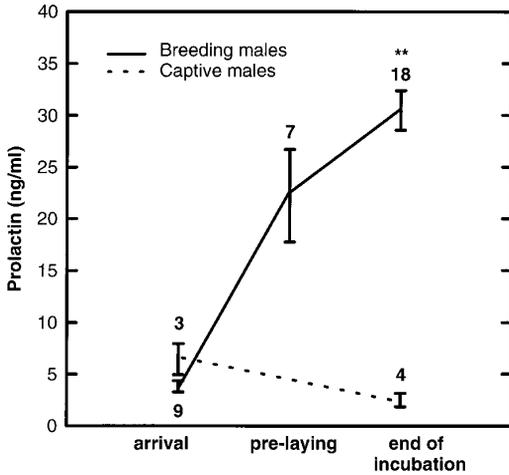
FIG. 4. Variation in mean (± SE) plasma prolactin in breeding males and captive (nonbreeding) males from arrival to the end of the incubation period (** = $P < 0.01$, U test). Sample sizes are given above the dots.

fense of the emperor penguin's only territory: the brood pouch (Isenmann and Jouventin, 1970). Persistence of high LH values during the parental care period related to aggressive or courting behavior has been shown in other species (Dittami, 1981, bar-headed goose, *Anser indicus;* Hannon and Wingfield, 1990, willow ptarmigan, *Lagopus lagopus*). In king penguins, however, LH values remain basal during both incubation (shared by the two mates) and the nestling period (Jouventin and Mauget, 1996). Two reasons may explain the difference in the LH patterns observed in king and emperor penguins during the brooding period. First, chick kidnapping has not been observed in king penguins; thus, parents do not need to protect their chick from failed breeders as in the case of the emperor penguins. If brooding behavior implies more aggressive behavior in emperor penguins than in king penguins, one might expect to find higher LH levels in the former than in the latter. Second, in king penguins brooding is shared equally by the two mates (Weimerskirch *et al.,* 1992), whereas in emperor penguins females do more brooding than males. As a consequence, LH levels are equal in both sexes of king penguins but tend to be higher in female emperor penguins.

Initiation of Prolactin Secretion

Several studies conducted on a wide range of bird species have shown that the initiation of prolactin secretion is associated with an increasing photoperiod (European starling, *S. vulgaris:* Dawson and Goldsmith, 1982, 1985; brown-headed cowbird, *Molothrus ater:* Dufty, Goldsmith, and Wingfield, 1986; gray partridge, *Perdix perdix:* Sharp, Massa, Bottoni, Lucini, Lea, Dunn, and Trochi, 1986; spotted sandpiper, *Actitis macularia:* Oring, Fivizzani, and El Halawani, 1986; white stork, *Ciconia ciconia:* Hall, Gwinner, and Bloesch, 1987). On the other hand, in the ring dove, no seasonal effects on prolactin secretion in male nonbreeders were detected (Lea, Sharp, Klandorf, Dunn, and Vowles, 1986). Furthermore, in the Bengalese finch, *Lonchura striata,* a nonseasonal breeder (Seiler, Gahr, Goldsmith, and Guttinger, 1992), the onset of incubation is not associated with increased photoperiod. In the winter breeding emperor penguin, prolac-
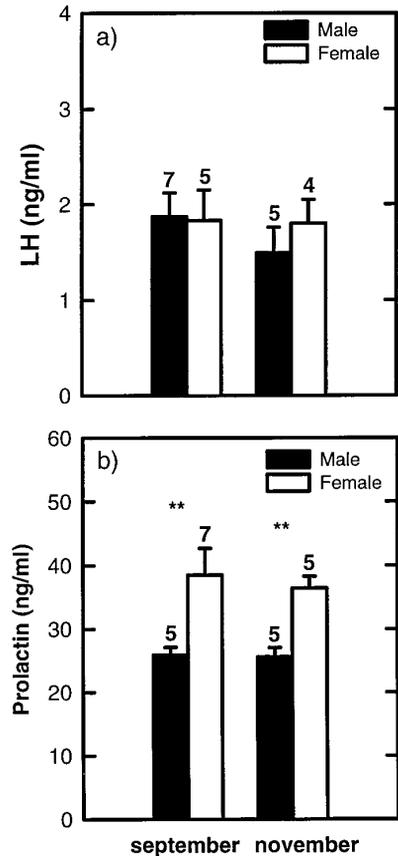

FIG. 5. a) Variation in mean plasma LH (± SE) in failed breeders. Sample sizes are given above bars. b) Variation in mean plasma prolactin (± SE) in failed breeders. Sample sizes are given above bars (** = $P < 0.01$, U test).

tin levels started to rise only once mating had occurred. These levels were basal in both sexes on arrival and stayed unchanged in captive nonbreeding males until the end of their 4-month fast. Such low levels may have been related to the stress induced by captivity, but Jouventin and Mauget (1996) showed that captivity did not significantly affect prolactin values in king penguins. On the other hand, from mating onward, plasma prolactin rises sharply in both sexes while photoperiod shortens.

Thus, in the emperor penguin, the onset of prolactin secretion does not appear to be directly induced by changes in photoperiod but rather may be dependent on whether the bird engages in reproductive behavior. As suggested in other bird species (turkey: Sharp, Lea, Chadwick, and Lake, 1981; ring dove: Cheng, 1979), we support the consensus view that in the breeding emperor penguin, the increased prolactin secretion may be a consequence of steroid-dependent sexual behavioral interactions between males and females. Since it does not appear that photoperiodic drive affects the onset and the maintenance of prolactin secretion, elevated steroids levels during the courtship period could be the determining factor for the onset of prolactin secretion in this species.

Maintenance of Prolactin Secretion in Breeders

In most bird species studied, prolactin secretion and parental care reinforce each other through tactile or visual stimuli (Buntin, 1996). In the ring dove, prolactin levels were shown to be maintained in the mate that was not incubating through the visual stimulus of the incubating partner (Lea *et al.,* 1986). The few pelagic seabirds studied so far do not appear to show any dependence on such stimuli to maintain prolactin secretion, and so some other factors may affect the secretion of this hormone. Hector and Goldsmith (1985) mentioned that in albatrosses there was no close relationship between prolactin secretion and the eggs and nest stimuli; the authors suggested that possibly prolactin secretion was endogenously timed. A fixed timing for prolactin secretion has also been suggested in the ring dove and the pied flycatcher (Silver, 1984; Silverin and Goldsmith, 1984). In these species, prolactin secretion drops when breeding failure occurs during incubation. However, prolactin secretion during incubation does not extend beyond a fixed time period, such as 15–18 days in the ring dove and 16–17 days in the flycatcher. This pattern of prolactin secretion has been defined as a "clock" (Lea *et al.,* 1986), i.e., this secretion was "of an endogenous nature, and

independent of social cues." Once eggs have hatched, the clock stops and the newly hatched chicks momentarily become the stimulatory factor for prolactin maintenance. In female emperor penguins, prolactin levels were elevated when they came back to the colony to brood their chicks, suggesting that prolactin levels increased while they were at sea for 2 months. Elevated prolactin titers were also maintained in males returning to the colony at the end of the brooding period, after a 3-week absence at sea.

These findings suggest that in the emperor penguin as in the king penguin (Jouventin and Mauget, 1996; Garcia *et al.,* 1996) and albatrosse (Hector and Goldsmith, 1985), prolactin secretion may be endogenously timed. Prolactin secretion independent of external stimuli may have evolved in pelagic seabirds to maintain parental care despite long absences from the breeding colony.

Maintenance of Prolactin Secretion after Breeding Failure

After chick loss, emperor penguins maintained elevated prolactin levels for up to 3 months after failure. The maintenance of such elevated prolactin values may represent the by-product of an endogenous regulation of prolactin secretion. Because of a massive failure during the brooding period, we did not collect data on birds rearing older, homeothermic chicks. Do such birds exhibit prolactin values similar to those observed in failed breeders in September–November? Among seabirds (albatrosses, gentoo, and macaroni penguins), prolactin secretion peaks during incubation and brooding and returns to basal levels during chick rearing. However, in the king penguin (Jouventin and Mauget, 1996; Garcia *et al.,* 1996), elevated prolactin levels are maintained throughout the chick-rearing period and are similar in failed breeders. In the closely related emperor penguin, one may expect prolactin concentration to be quite similar in chick-rearing birds and failed breeders. The maintenance of elevated prolactin levels after chick loss is known to have a depressive effect on gonadotropin secretions (Sharp *et al.,* 1979) and may preclude emperor penguins from relaying too late in the season, because late-breeding birds have to cope with another energy demanding event, the molt (Cherel, Charassin, and Challet, 1994).

Sex Difference in Prolactin Values

In the emperor penguin, parental duties do not start at the same time for males (incubation) and females

(brooding), and it can be suggested that the rise in prolactin secretion occurs earlier in males than in females. This is reinforced by our observation that males had higher prolactin values than females during the prelaying period. Such uncoupled timing of the rise in prolactin is in contrast with previous findings in other seabirds in which the timing of prolactin secretion is roughly similar in each sex (Hector and Goldsmith, 1985; Williams and Sharp, 1993; Hall, 1986; Cherel *et al.,* 1994).

In most bird species, prolactin levels are higher in the sex that invests more in parental duties (Ball, 1991; Oring, Fivizzani, Colwell, and El Halawani, 1988). In seabird species in which parental duties are equally shared, similar prolactin levels are found in males and females: gray-headed and black-browed albatrosses (*Diomedea chrysostoma* and *D. melanophrys,* Hector and Goldsmith, 1985) and macaroni penguins (*Eudyptes chrysolophus;* Williams and Sharp, 1993), but in several cases, the highest values are found in females during most of the breeding period (Cape gannet, Hall, 1986 (nonsignificant trend); gentoo penguin, *Pygoscelis papua,* Williams and Sharp, 1993; wandering albatross, *D. exulans,* Hector and Goldsmith, 1985; king penguin, Cherel *et al.,* 1994). Male emperor penguins assume, on average, 93 days of parental care from laying to departure of the chick (incubation + chick rearing) versus 39 days for females (brooding + chick rearing). With such unbalanced roles in parental duties, the males may be expected to show the highest prolactin levels, but yet, female prolactin levels were superior to those of males during brooding and even after breeding failure. Such a difference may arise from the type of parental behavior performed by each sex. Female emperor penguins assume the whole brooding period and may need high prolactin levels to successfully perform this behavior. Such a connection between high prolactin levels and brooding behavior has been shown in other species, like the pied flycatcher and the ring dove, in which prolactin levels increase momentarily after the replacement of eggs by newly hatched chicks (Silverin and Goldsmith, 1990; Lea *et al.,* 1986). We cannot rule out the possibility that incubating males may have higher prolactin titers than those departing at the end of incubation (to avoid egg desertion, male emperor penguins were not sampled). However, in incubating king penguins, prolactin values were shown to increase from the beginning to the end of the incubation shift (Cherel *et al.,* 1994).

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