



## Stress, prolactin and parental investment in birds: A review

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### ABSTRACT

In this paper, we review the relationships that link avian parental behavior, stress (acute or chronic) and energetic constraints to the secretion of prolactin, the 'parental hormone'. Prolactin secretion is stimulated by exposure of the parent to tactile and visual stimuli from the nest, the eggs or the chicks, while prolactin facilitates/stimulates the expression of parental behaviors, such as incubating, brooding or feeding. Because of this role of prolactin in the expression of parental behaviors, we suggest that absolute circulating prolactin levels may reflect to the extent to which individuals provide parental care (i.e., parental effort). Stressors and energetic constraints (acute or chronic) depress prolactin levels ('the prolactin stress response') and this may be adaptive because it may disrupt the current parental effort of an individual and promote its survival. Alternatively, an attenuation of the prolactin stress response can be considered as a hormonal tactic permitting the maintenance of parental care to the detriment of parental survival during stressful situations. Therefore, we suggest that the magnitude of the prolactin stress response may reflect parental investment. Finally, we detail the interaction that links corticosterone, prolactin and stress in bird parents. We suggest that corticosterone and prolactin may mediate different components of the stress response, and, therefore, we emphasize the importance of considering both hormones when investigating the hormonal basis of parental investment.

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### 1. Introduction

Sometimes, during the parental phase of the breeding cycle, birds have to cope with a sudden unpredictable stressor, such as an attack by a predator or deleterious climatic events (environmental perturbations). In addition to these stressors, the parental phase is also associated with predictable changed energetic demands, related to the need to feed chicks, to fast while incubating or to defend territory against predators. All these stressors and energetic constraints negatively affect a parent's survival either indirectly, by reducing the energy available for self-maintenance processes, or directly, by causing mortality. Vertebrates have evolved behavioral and physiological responses to these stressors and predictable changes in energetic demands in order to actively reduce their adverse consequences on survival (the concept of allostasis and stress response, Wingfield et al., 1998; McEwen and Wingfield, 2003; Landys et al., 2006). At the proximate level, allostasis and stress responses are primarily mediated by the same neuro-endocrine mechanisms involving the hypothalamo–pituitary–adrenal axis (HPA), catecholamines and cytokines (McEwen and Wingfield, 2003). These mechanisms mediate physiological and behavioral changes (metabolism, immunity, escape behavior,

etc. Sapolsky et al., 2000), that differ depending on the duration of exposure to the stressors and energetic constraints (i.e., acute vs. chronic stress responses, Landys et al., 2006). These changes redirect available resources (energy and time) to processes that maximize a parent's survival (Wingfield et al., 1998; Ricklefs and Wikelski, 2002).

Among the most consistent effects of acute or chronic stressors and energetic constraints on parental birds is the reduction or disruption of parental behavior (Wingfield et al., 1998; Sapolsky et al., 2000; Wingfield and Sapolsky, 2003) and parental effort (i.e., the amount of resources allocated to parental activities). Although a reduction in parental effort favors the survival of parents, life-history theory predicts that parental behavior should not be reduced when the fitness value of the current reproductive event is high relative to the fitness value of future reproductive events (Stearns, 1992). For this reason, it can be beneficial for the fitness of a parent to attenuate or suppress mechanisms that reduce parental behavior (Wingfield and Sapolsky, 2003). Consistent with this view, a hormonal component of the stress response—the secretion of corticosterone, a hormone known to disrupt parental behavior—is attenuated or even suppressed when the fitness value of the current reproductive event is relatively high (Wingfield and Sapolsky, 2003; Bokony et al., 2009).

In recent decades, the study of allostasis and stress (acute or chronic, *sensu* McEwen and Wingfield, 2003) in birds has benefited from investigation of their primary mediator—corticosterone

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(Ricklefs and Wikelski, 2002; Wingfield and Sapolsky, 2003; Landys et al., 2006). The corticosterone stress response consists of a quick and dramatic increase in corticosterone levels (the acute stress response), that results from the activation of the HPA axis (Sapolsky et al., 2000). This increase mediates behavioral and physiological adjustments in response to stressors or perturbations that reduce reproductive activities and promote survival (Wingfield et al., 1998; Landys et al., 2006). The magnitude of the acute corticosterone stress response, therefore, has been suggested as a relevant measure of parental investment in birds (Wingfield and Sapolsky, 2003; Ricklefs and Wikelski, 2002; Lendvai et al., 2007; Lendvai and Chastel, 2008; Bokony et al., 2009), where parental investment refers to the concept of allocating resources to parental activities and away from other life-history components (i.e., survival). When an individual has successfully coped with a stressor, its corticosterone level returns to a low concentration and reproductive activities are thus restored. However, individuals are not always able to cope with these stressors despite the activation of the acute stress response and, in these situations, elevated corticosterone levels are maintained over a prolonged period (the chronic stress response). This chronic stress response inhibits and suppresses reproduction to a dramatic extent in order to promote homeostasis (McEwen and Wingfield, 2003; Wingfield and Sapolsky, 2003; Sapolsky et al., 2000). Recently, it has been suggested that another hormone, prolactin, could be involved in mediating the trade-off between parental effort and self-maintenance (Chastel et al., 2005). Prolactin has a wide range of biological actions (Freeman et al., 2000), and may play a role in mediating the effect of stressors and environmental perturbations on avian parental effort for two reasons. First, the concentrations of circulating prolactin are depressed by acute and chronic stressors (Chastel et al., 2005) and by energetic constraints (Cherel et al., 1994; Angelier et al., 2007a), and secondly, prolactin is involved in the expression of parental behavior (Buntin, 1996; Vleck, 1998).

In this review we emphasize the potential ability of prolactin to mediate parental investment in birds (i.e., the trade-off between survival and parental effort). We review (1) the neurobehavioral interactions that link avian parental behavior and prolactin secretion, (2) the effects of stressors (acute and chronic) and energetic constraints on prolactin levels during the parental phase and (3) the modulation of circulating prolactin levels by acute stressors. Based on these observations, we develop the hypothesis that the “prolactin stress response” can be used as a physiological tool to monitor parental effort and test specific ecological hypotheses related to parental investment in birds. Finally, we emphasize the importance of considering possible interactions between corticosterone and prolactin in the regulation of parental investment in birds.

## 2. Prolactin secretion during the parental phase

Prolactin is secreted by anterior pituitary cells called lactotrophs, under the stimulatory control of vasoactive intestinal polypeptide (VIP), which is synthesized in basal hypothalamic neurons and released from the median eminence into the hypophysial portal vasculature. The activities of basal hypothalamic VIP-ergic neurons in turn, are controlled by neural pathways containing dopamine, serotonin and opioids that signal environmental and intrinsic information (see Sharp et al., 1998; Freeman et al., 2000; Sockman et al., 2006 for further details).

Although prolactin levels increase over the course of the breeding season as a result of photostimulation (Dawson and Goldsmith, 1982), a further increase in prolactin secretion in many birds is stimulated by increased basal hypothalamic VIP-ergic activity triggered by visual and tactile stimuli from the nest, the eggs or the

chicks (El Halawani et al., 1986; Book et al., 1991; Hall, 1987; Sharp et al., 1998; Fig. 1). However, prolactin secretion is relatively independent of these stimuli in some birds such as pelagic seabirds, which are absent from the nest for prolonged periods. In these species, increased prolactin secretion results from an endogenous cycle (Hector and Goldsmith, 1985; Lormée et al., 1999; Vleck et al., 2000; Angelier et al., 2006a).

## 3. Prolactin and parental behavior

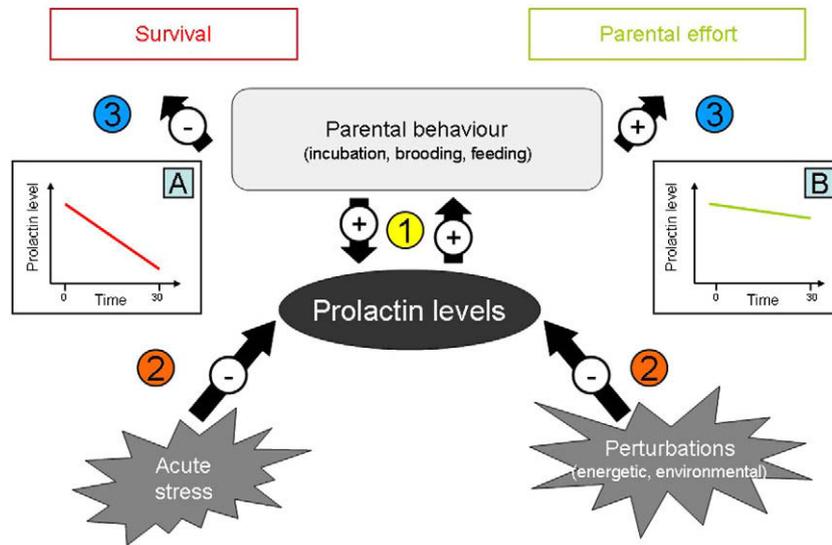
### 3.1. Prolactin levels during the parental phase

In breeding birds, an increase in prolactin secretion is involved in the transition from sexual to parental activity (Sharp et al., 1998; Sockman et al., 2006). Prolactin levels rise at the onset of laying and stay elevated during a part and, sometimes, during the entire parental phase and then decline rapidly to return to pre-laying levels (Hall, 1987; Sharp et al., 1988; Vleck, 1998; Lormée et al., 2000; Deviche and Sharp, 2001; Sockman et al., 2006). Thus, prolactin levels are most elevated during the period of parental care (Buntin, 1996) and this is reflected in differences in circulating prolactin in birds with different parental behaviors. First, in birds with precocial young, plasma prolactin declines shortly after hatching, stays only moderately elevated during the brooding period and thereafter decreases, whereas in birds with altricial young, plasma prolactin remains elevated after hatching while the chick are being intensively fed and guarded. Second, among species in which parental care is provided only by the female, plasma prolactin is more elevated in females than in males while conversely, in species in which parental care is provided only by the male, plasma prolactin is higher in males than in females during the parental phase of the breeding cycle (reviewed in Sharp et al., 1998; Vleck, 1998).

### 3.2. Prolactin stimulates/facilitates the expression of parental behavior

In addition to these sex- and stage-dependent variations in prolactin levels, other studies support the view that prolactin is involved in the expression of avian parental care. Laboratory studies demonstrate that injection of prolactin stimulates the expression of brooding, feeding and protective behaviors in parental Ring doves, *Streptopelia risoria*, and of incubation behavior in turkey hens, *Meleagris gallopavo* (Buntin et al., 1991; Youngren et al., 1991; Wang and Buntin, 1999). Further, experimental reduction of circulating prolactin (or VIP) in the turkey and domestic hen inhibits incubation behavior (Sharp et al., 1989; El Halawani et al., 1995).

Many studies in wild birds suggest a role for prolactin in the expression of parental behaviors. A positive correlation between the intensity/quality of parental care and plasma prolactin concentrations has been observed in many parental birds (Sharp et al., 1988; Duckworth et al., 2003; Van Roo et al., 2003; Angelier et al., 2007a, in press-a; Boos et al., 2007) and cooperative breeders (Vleck et al., 1991; Schoech et al., 1996; Khan et al., 2001). For instance, in the cooperatively breeding Florida Scrub-Jays (*Aphelocoma coerulescens*), the prolactin levels in helpers are positively correlated with the rate of nestling provisioning (Schoech et al., 1996). Further, baseline prolactin levels appear to positively correlate with phenotypic quality and age-related breeding performances (Deviche et al., 2000; Duckworth et al., 2003; Prévault et al., 2005; Angelier et al., 2006b, 2007a, 2007b; Christensen and Vleck, 2008) while other studies support the view that prolactin maintains willingness of parents to stay on and to return to the nest (Hector and Goldsmith, 1985; Lormée et al., 1999; Vleck et al., 2000; Angelier et al., 2006a, 2007a, in press-a).



**Fig. 1.** A model to show how the prolactin stress response can be used to assess the extent to which a parental bird allocates limited resources between parental and self-maintenance behaviors when subject to acute or chronic stressors (energetic or environmental perturbations). (1) Changes in circulating prolactin levels modulate parental behavior; increased prolactin maintains/stimulates these behaviors while decreased prolactin weakens them. Baseline prolactin levels reflect parental effort (i.e., to what extent individuals provide parental cares). (2) Prolactin levels decrease in response to acute and chronic stressors (prolonged energetic constraints or environmental perturbations). (3) Available energetic resources are allocated to support parental survival and parental effort, and the portioning of this allocation favors either the survival of the parents or of the young. The rate of decrease in plasma prolactin response to a standardized stress protocol (capture followed by 30 min restraint) (A, B) is directly related to the motivation to maintain parental effort. (A) A large decrease in prolactin levels reduces parental investment and may therefore favor survival to the detriment of parental effort. (B) An attenuation of this decrease in prolactin levels may favor parental effort to the detriment of survival (high parental investment).

Some examples of the evidence for a role for prolactin in the expression of parental behaviors in wild birds include the observations that an experimental increase in prolactin induces parental behavior in Willow Ptarmigans, *Lagopus lagopus*, and American Kestrels, *Falco sparverius* (Pedersen, 1989; Sockman et al., 2000) while in the Emperor Penguin, *Aptenodytes forsteri*, an experimental reduction of prolactin levels results in a lower frequency of kidnapping behaviors, a frequent alloparental behavior in this species (Angelier et al., 2006a). Finally, prolactin is also involved in ultimate parental decisions such as abandonment of the eggs or chicks (Cherel et al., 1994; Angelier et al., 2007a; Groscolas et al., 2008). For instance, low prolactin levels are associated with chick abandonment in the Red-footed Booby, *Sula sula* (Chastel and Lormée, 2002).

### 3.3. Prolactin and parental behavior: a complex relationship

Recent studies suggest that the relationship between the expression of parental behavior and prolactin levels could be context-dependent. Although elevated circulating prolactin is required for the expression of parental behaviors (Buntin, 1996; Vleck, 1998), it is not sufficient since prolactin does not stimulate parental behavior in the absence of increased gonadal steroid hormones, i.e., if birds are not in a reproductive state (El Halawani et al., 1986). In addition, other intrinsic factors such as breeding experience can affect the capacity of prolactin to stimulate parental behavior in birds. Thus, an experimental increase in prolactin levels stimulates parental behavior in reproductively experienced but not in inexperienced Ring doves (Buntin et al., 1991). Further studies are needed to determine what factors (intrinsic and environmental) affect the capacity of prolactin to facilitate the expression of parental care in birds. There is growing evidence that the relationship between parental behavior and prolactin levels is non-linear and depends on a threshold value of prolactin levels. Thus, parental care might be maximally expressed after circulating prolactin concentrations reach an upper threshold value, but be

low when prolactin concentrations are below this threshold (Angelier et al., 2006a, 2007a; Boos et al., 2007).

Our global understanding of the action of prolactin on the expression of parental behavior would benefit from further physiological and laboratory studies. The effect of prolactin on parental behavior is mediated through the binding to specific brain receptors and through the clearance rate of the hormone in the body (Freeman et al., 2000). However, research on the mechanisms of action of prolactin in the avian brain are currently limited. The binding characteristics and distribution of prolactin receptor in the brain has been well studied in the ring dove (Buntin et al., 1993) and a few studies have examined whether the concentration of prolactin receptor mRNA in specific brain regions varies with the expression of parental care in the domestic hen (Ohkubo et al., 1998a, 1998b). Moreover, another study has demonstrated that different types of prolactin receptor transcripts occur in the turkey (Pitts et al., 2000). It is unknown whether, or how ecological factors (breeding stage, age, experience, etc.) affect the physiology of these receptors in non-poultry birds. Future studies of variations in prolactin clearance rate, prolactin receptor affinity and prolactin receptor location, numbers and density may explain, at the physiological level, why the effects of prolactin on parental behavior are context-dependent and non-linear.

## 4. Acute stress, energetic constraints and prolactin levels

### 4.1. Acute stress

Plasma prolactin levels rapidly increase during acute stress in mammals, and this rise in plasma prolactin levels is often considered part of the classical stress response (De Vlaming, 1979). However in birds, prolactin levels often decrease in response to short-term stressors such as handling, restraint or injections (Turkey, *Meleagris gallopavo*, Opel and Proudman, 1986; Semipalmated sandpiper *Calidris pusilla*, Gratto-Trevor et al., 1991). Recently, Chastel et al. (2005) showed that a standardized capture/handling stress protocol results in a decrease in prolactin levels

in Black-legged kittiwakes (*Rissa tridactyla*). Moreover, several recent studies reported the same pattern: plasma prolactin levels decrease by 20–28% over a 30-min stress protocol in many species (Snow petrel, *Pagodroma nivea*, Angelier et al., 2007a, in press-b; Glaucous gull, *Larus hyperboreus*, Verreault et al., 2008; Kerguelen shag, *Phalacrocorax verrucosus*, Cook, Bost and Chastel, unpublished results; House sparrow, *Passer domesticus*, Lendvai and Chastel, unpublished manuscript). The stress-induced decrease in prolactin levels is non-linear. In Black-legged Kittiwakes, prolactin levels slightly increase during the few minutes following the initiation of acute stress before significantly decreasing (Chastel et al., 2005). This suggests that the effect of acute stress on prolactin secretion, synthesis or clearance rate might vary with the duration of stress exposure. However, this interpretation requires further investigation since the detailed kinetics of prolactin levels in response to acute stress has been examined in only one species (i.e., the Black-legged kittiwake).

#### 4.2. Prolonged stressors and energetic constraint

In some circumstances, bird parents are exposed to prolonged stressors and energetic constraints. These perturbations/constraints can be predictable (e.g., prolonged fasting associated with incubation of the eggs) or unpredictable (e.g., prolonged reduction in food availability), but there is evidence that both result in a decrease in prolactin levels. The depressive effect of prolonged fasting on prolactin levels is well documented. Thus, in some seabirds and wildfowls, circulating prolactin levels decrease in response to large and prolonged depletion of body reserves that can occur during incubation and chick-brooding (Cherel et al., 1994; Criscuolo et al., 2002; Jonsson et al., 2006; Angelier et al., 2007b; Groscolas et al., 2008). Other long-lasting environmental stressors can also result in reduced prolactin levels. For instance, Delehanty et al. (1997) showed that severe and prolonged drought is associated with low prolactin levels in Wilson's Phalaropes (*Phalaropus tricolor*). Moreover, the chronic stress induced by captivity can also result in a significant decrease in prolactin levels as for example, the 60% decrease in prolactin levels within a few days of captivity in Common Eiders, *Somateria mollissima* (Criscuolo et al., 2005).

### 5. Modulation of prolactin levels

#### 5.1. Significance of prolactin levels in terms of parental effort and parental investment

Parental effort is classically associated with costs of survival because the resources allocated to parental care are no longer available for self-maintenance processes (Stearns, 1992). Because prolactin facilitates/stimulates the expression of parental care in birds (see Section 3), prolactin levels potentially reflect the extent to which resources are allocated to parental activities and may, therefore, be a useful indicator of parental effort and parental investment.

In the field, physiologists and ecologists usually measure baseline prolactin levels within few minutes of capture (i.e., when prolactin levels are not yet affected by the stress of capture/handling). Although baseline prolactin levels potentially reflect the extent to which individuals provide parental care (parental effort, Fig. 1), they do not reflect how available resources are shared between self-maintenance and parental processes (i.e., parental investment). Measuring parental investment requires monitoring individuals to determine how they divide available resources between parental effort and self-maintenance behaviors when these behaviors cannot be maintained at the maximal level (i.e., when resources are limited or in a stressful situation). Recently,

Chastel et al. (2005) suggested using a standardized stress protocol to monitor the rate of reduction in circulating prolactin levels as a measure of the reduction in parental effort in response to a life-threatening situation (Fig. 1). A stress-induced decrease in prolactin levels in a parental bird, faced with limited resources or a severe acute stressor can be considered to be adaptive by disrupting the current parental effort to promote parental survival and prospects of future reproduction (Chastel et al., 2005). For example, a large decrease in prolactin levels in response to a standardized stress protocol is associated with the ultimate decision to desert the nest in incubating Snow Petrels (Angelier et al., 2007a). On the other hand, an attenuation of the prolactin response to stress can be considered as a hormonal tactic permitting the maintenance of parental cares and maximizing current parental effort during stressful situations. Supporting this hypothesis, parental birds attenuate the prolactin stress response in order to maintain elevated prolactin levels in a stressful situation when the current reproductive event has a large fitness value (incubation: Angelier et al., 2007a, in press-b; chick-rearing: Chastel et al., 2005). It is therefore proposed that the magnitude of the decrease in prolactin levels in parental birds in response to a stress protocol is directly related to their current parental investment (Fig. 1).

To sum up, we suggest that (1) baseline prolactin levels in parenting birds may indicate parental effort (the amount and quality of parental cares provided), and that (2) the prolactin response to a standardized stress protocol may reflect parental investment (the ability to maintain parental care when facing stressors or deleterious situations).

#### 5.2. Baseline prolactin levels

In this section, we focus on four variables which have been shown to affect prolactin baseline levels and show how these can be informative to ecologists investigating the influence of environmental and intrinsic variables on parental effort and reproductive performance.

First, baseline prolactin levels have been shown to differ between breeding seasons (Delehanty et al., 1997; Deviche and Sharp, 2001; Angelier et al., 2006a), suggesting that year to year differences in environmental conditions affect prolactin levels and may affect breeding success. For example, in Wilson's phalaropes Delehanty et al. (1997) found low prolactin levels associated with drought (i.e., prolonged deleterious environmental perturbation) and with a concomitant low breeding success. Although only a few studies have examined prolactin levels in contrasting environmental situations, it is likely that baseline prolactin levels may reflect environmental conditions and parental effort and predict reproductive performances of bird populations.

Secondly, several studies have reported that parental birds in poor body condition have lower prolactin levels than birds in good body condition (Weimerskirch and Cherel, 1998; O'Dwyer et al., 2006; Jonsson et al., 2006). Low prolactin levels in birds in poor body condition probably explain why they provide poor parental care (Groscolas et al., 2008).

Thirdly, in photoperiodic species, baseline prolactin levels are also determined by the annual cycle of changing photoperiod and by the development and dissipation of photorefractoriness (reviewed in Sockman et al., 2006). Baseline prolactin levels increase as the breeding season proceeds and, because of the inhibitory effect of prolactin on egg laying (El Halawani et al., 1991; Sharp et al., 1988), this increase may explain, at the proximate level, reduced clutch size of clutches laid late in the breeding season (Sockman et al., 2006).

Finally, there is growing evidence that baseline prolactin levels are affected by breeding experience. Thus, inexperienced parents have lower baseline prolactin levels than more experienced ones

(Deviche et al., 2000; Angelier et al., 2006b, 2007b; Christensen and Vleck, 2008). This observation suggests that inexperienced breeders may show lower parental effort than more experienced birds. At the proximate level, the influence of experience on prolactin levels may partly explain why inexperienced birds usually reproduce less well than more experienced ones.

In summary, these observations suggest that differences in baseline prolactin levels may explain differences in reproductive performance and parental effort between individuals and populations. However, in some situations, baseline prolactin levels may vary between individuals in the absence of apparent difference in parental behavior (e.g., sexual differences in prolactin levels in seabirds, Hector and Goldsmith, 1985; Vleck, 1998; Angelier et al., 2006b, 2007a, 2007b). Measuring baseline prolactin levels may be useful in conservation biology because it could potentially allow a better understanding of how environmental changes can mechanistically affect the reproductive performances of wild birds.

### 5.3. Modulation of the acute stress response

In this section, we review the evidence for the modulation of prolactin levels in response to a standardized stress protocol. We propose that the prolactin stress response can be used to test hypotheses related to life-history theory and, specifically, to parental and reproductive investment in birds. This concept was first developed and tested by Chastel et al. (2005) who compared the effect of a standardized stress protocol on the prolactin levels Black-legged kittiwakes, which were either failed breeders or were rearing chicks. Baseline prolactin levels are elevated both in birds caring for chicks and in failed breeders, which remained in the colony to defend their nests against prospecting conspecifics. Defending the nest site increases the probability of successfully reproducing during the next breeding season. However the fitness value to a failed breeder of maintaining attendance at the nest site is less than for a successful breeder. Therefore, life-history theory predicts that failed breeders should be less inclined to stay on the nest and maintain elevated prolactin levels than parents when facing life-threatening situations. Consistent with the prolactin stress response hypothesis, kittiwake parents caring for young attenuated their prolactin stress response (9% decrease in prolactin) less than in failed breeders (41% decrease in prolactin) in response to the same handling stress.

Following this initial study, modulation of the prolactin stress response was investigated in relation to age-related variations in parental investment. As organisms age, the fitness value of current reproduction is expected to be greater relative to the fitness value of future reproduction and survival because future reproductive opportunities are expected to decline (Stearns, 1992). Thus, evolutionary theory predicts that parental investment should increase with advancing age as the prospects for future breeding opportunities decrease. Consistent with this prediction, the prolactin stress response to a standardized stress protocol in Snow Petrels was less in old than in young parental birds (Angelier et al., 2007a). The Black-legged Kittiwake and Snow Petrel examples illustrate perfectly how the prolactin stress response reflects risk taking strategies and, thus, parental or reproductive investment (Fig. 1). This suggests that birds attenuate their prolactin response to acute stress to ensure that reproduction is not inhibited when the fitness value of current the reproductive event is high (the 'brood value hypothesis'; Heidinger et al., 2006; Lendvai et al., 2007; Lendvai and Chastel, 2008; Bokony et al., 2009). The prolactin response to acute stress in breeding birds may therefore mediate some life-history trade-offs as does the more extensively studied corticosterone stress response (Ricklefs and Wikelski, 2002; Wingfield and Sapolsky, 2003; Bokony et al., 2009).

## 6. Do corticosterone and prolactin interact to mediate parental investment?

### 6.1. Endocrine responses to acute stressors

To our knowledge, there is no evidence that prolactin and corticosterone responses to acute stressors are mechanistically related. Indeed, no study has reported any correlation between these two acute stress responses in bird parents, and the short-term secretions of these two hormones are known to be primarily governed by different neuro-endocrine pathways (Sharp et al., 1998; Wingfield and Sapolsky, 2003). In addition, some studies have reported that the prolactin stress response, but not the corticosterone stress response, is modulated according to environmental and life-history variables (Chastel et al., 2005; Angelier et al., 2007a), and a short-term experimental increase of corticosterone levels does not affect prolactin levels in chick-rearing Snow Petrels (Angelier et al., in press-b). All these results support the idea that the corticosterone and prolactin stress responses are not mechanistically related. Therefore, we suggest that these two hormones mediate two independent components of the acute stress response. According to the existing literature, the stress-induced increase in corticosterone levels mediates physiological and behavioral changes that promote energetic balance (Sapolsky et al., 2000; Landys et al., 2006), whereas the magnitude of the decrease in prolactin levels would determine to what extent individuals reduce their parental effort (Chastel et al., 2005; Angelier et al., 2007a).

### 6.2. Chronic environmental and energetic perturbations

In contrast to the responses of corticosterone and prolactin to acute stress, there is correlative and experimental evidence that prolactin and corticosterone responses to prolonged stressors or energetic constraints are mechanistically connected. Thus, baseline corticosterone and prolactin levels are correlated in some cases (Angelier et al., 2007b, in press-b), and prolonged environmental perturbations and energetic constraints affect corticosterone and prolactin levels concomitantly in parental birds (Delehanty et al., 1997; Wingfield et al., 1998; Angelier et al., 2007b; Groscolas et al., 2008). In addition, prolactin levels decrease in response to a prolonged experimental administration of corticosterone in parental birds (Crisuolo et al., 2005; Angelier et al., in press-a) and laboratory rodents (Freeman et al., 2000), demonstrating an inhibitory action of corticosterone on prolactin synthesis or secretion. However, this inhibitory action of corticosterone on plasma prolactin is probably complex and deserves further examination because prolactin levels decrease only slowly and progressively in response to corticosterone manipulation (Angelier et al., in press-a).

At the ultimate level, maintenance of elevated corticosterone levels during a prolonged time period reflects an allostatic overload (a chronic stress), which is associated with dramatic costs in terms of survival (McEwen and Wingfield, 2003; Landys et al., 2006). In this situation, parents have to reduce their energetic needs in order to return to homeostasis. This can be achieved by reducing prolactin levels and, therefore, parental effort through an inhibitory effect of corticosterone on prolactin secretion. Therefore, corticosterone could govern the ultimate decision to reduce or suppress parental effort by inhibiting prolactin secretion. To conclude, both corticosterone and prolactin are very likely to mediate parental effort and parental investment in birds (Koch et al., 2004; Chastel et al., 2005; Crisuolo et al., 2005; Angelier et al., 2007a, in press-a, in press-b; Groscolas et al., 2008). Consequently, it appears essential in the future to better understand how these two

hormones (1) are mechanistically related and (2) interact to affect specific physiological and behavioral components associated with parental activity.

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