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Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review

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ABSTRACT

This article is part of a Special Issue "Parental Care".

In vertebrates, adjustments of physiology and behavior to environmental changes are often mediated by central physiological mechanisms, and more specifically by hormonal mechanisms. As a consequence, these mechanisms are thought to orchestrate life-history decisions in wild vertebrates. For instance, investigating the hormonal regulation of parental behavior is relevant to evaluate how parents modulate their effort according to specific environmental conditions. Surprisingly and despite being classically known as the 'parental hormone', prolactin has been overlooked in birds relative to this context. Our aim is to review evidence that changes in prolactin levels can mediate, at least to some extent, the response of breeding birds to environmental conditions. To do so, we first examine current evidence and limits for the role of prolactin in mediating parental behavior in birds. Second, we emphasize the influence of environmental conditions and stressors on circulating prolactin levels. In addition, we review to what extent prolactin levels are a reliable predictor of breeding success in wild birds. By linking environmental conditions, prolactin regulation, parental behavior, and breeding success, we highlight the potential role of this hormone in mediating parental decisions in birds. Finally, we also review the potential role of prolactin in mediating other life history decisions such as clutch size, re-nesting, and the timing of molt. By evaluating the influence of stressors on circulating prolactin levels during these other life-history decisions, we also raise new hypotheses regarding the potential of the prolactin stress response to regulate the orchestration of the annual cycle when environmental changes occur. To sum up, we show in this review that prolactin regulation has a strong potential to allow ecological physiologists to better understand how individuals adjust their life-history decisions (clutch size, parental behavior, re-nesting, and onset of molt) according to the environmental conditions they encounter and we encourage further research on that topic.

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Introduction

In birds, all species exhibit some kind of parental behaviors, the functions of which are to produce offspring of high quality that will be able to survive and reproduce in their environment. Among others, these functions involve incubation behavior, protecting the egg or the chick, and provisioning the brood (Newton, 1989; Clutton-Brock, 1991). Although they obviously provide fitness benefits to the parents, all these behaviors are also costly because they require time and energy that cannot be allocated to self-maintenance and survival unless that breeding attempt is abandoned. Because of this life-history trade-off, it is predicted that parents should adjust their parental effort in order to optimize their fitness (Stearns, 1992). As a consequence, parental behavior and physiology should be modulated according to different variables (McNamara and Houston, 1996), such as the energetic needs of the eggs/chicks, the state of the parent (e.g. condition, age), the parental effort of the mate, and environmental conditions (e.g. predation risk, food availability).

Parental effort is primarily mediated by physiology, and more specifically by neurological and hormonal mechanisms (Zera and Harshman, 2001; Ricklefs and Wikelski, 2002; Wingfield et al., 2008). Because hormones are pleiotropic, the activation of specific endocrine mechanisms can for example redirect the allocation of resources from one component (e.g. reproduction) towards another (e.g. self-maintenance) when resources are limited. Therefore, hormonal mechanisms can orchestrate life-history decisions and investigating the hormonal regulation of parental physiology is relevant to evaluate how parents modulate their effort according to specific environmental conditions. In the context of parental effort, several hormones have been studied. Among them, testosterone and corticosterone have for example drawn a lot of attention from environmental endocrinologists (Wingfield et al., 1990, 1998; Bonier et al., 2009; Angelier and Wingfield, 2013). Surprisingly and despite being classically known as the 'parental hormone' (Hall et al., 1986; Buntin, 1996; Vleck, 1998; Sockman et al., 2006), prolactin has been overlooked in

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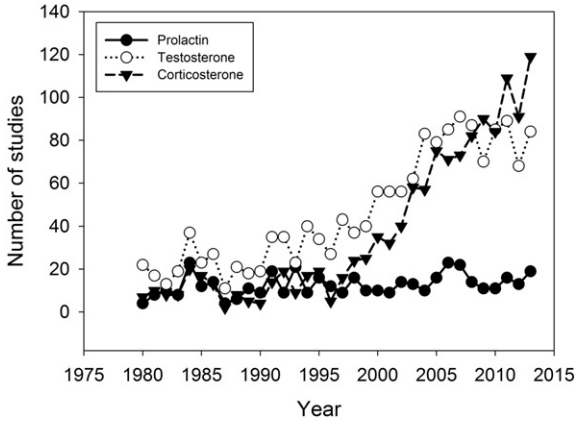

Fig. 1. Trends in the number of studies published each year on different hormones from 1980 to 2013. These numbers were found by conducting a search in ISI Web of Knowledge (search terms: corticosterone, testosterone, prolactin and bird, search date: January 15 2015).

birds relative to this context, maybe because of the technical difficulties to assay this specific avian peptide. For example, the numbers of studies focusing on corticosterone, testosterone or prolactin were roughly similar in the early eighties (Fig. 1). However, the number of studies on corticosterone and testosterone has exponentially increased while the number of studies on prolactin has remained steady (Fig. 1).

Contrary to testosterone and corticosterone that are well-known for their fitness costs (e.g. reduced immunity and survival), prolactin has rarely been perceived as being involved in life-history trade-offs, perhaps explaining this lack of interest from ecological physiologists. Variations in prolactin levels were thought to be mainly related to reproductive stimuli (Hall et al., 1986; Sharp et al., 1998), photoperiod changes (Sharp et al., 1998; Dawson et al., 2001), and modifications in parental behavior (Buntin, 1996; Vleck, 1998). In the 2000s, environmental stressors have, however, been suggested to dramatically affect circulating prolactin levels in parent birds (Chastel et al., 2005; Angelier et al., 2013). Because prolactin is involved in the expression of parental behavior (Silver, 1984; Hall et al., 1986; Buntin, 1996; Vleck, 1998; Sockman et al., 2006), this important finding has suggested that changes in prolactin levels could also mediate individual short-term response to variations in environmental conditions (Angelier and Chastel, 2009).

Since these findings, the prolactin stress response has been increasingly studied in wild birds because of its potential implication in the regulation of parental effort in a context of environmental changes. As a consequence, our understanding of the role of prolactin in mediating parental decisions has improved although it is still subject to debate (Angelier and Chastel, 2009; Williams, 2012). Our aim is to review evidence that changes in prolactin levels can mediate the response of parent birds to environmental conditions. To do so, we will first examine evidence and limits for the role of prolactin in mediating parental behavior in birds. Second, we will emphasize the influence of environmental conditions and stressors on circulating prolactin levels. In this second part, we will also examine to what extent prolactin levels are a reliable predictor of breeding success in wild birds. We will additionally review evidence of a possible disruption of prolactin secretion by environmental contaminants. By linking environmental conditions, stress, prolactin regulation and breeding success, we will highlight the potential role of this hormone in mediating allostasis in parent birds. Finally, we will also review the potential role of prolactin in mediating other life history decisions such as clutch size (Sockman et al., 2006; Ryan et al., 2015) and the timing of molt (Dawson, 2006). By evaluating the influence of stressors on circulating prolactin levels during these stages, we will also raise new hypotheses regarding the potential of prolactin to regulate the orchestration of the annual cycle when environmental changes occur.

Prolactin and parental behavior

Since the first studies conducted on prolactin in birds, this hormone has been known as 'the parental hormone' (Riddle, 1963). There is strong evidence that this hormone is tightly linked to the parental phase in birds (Buntin, 1996) and the regulation of parental behavior by prolactin has benefited from numerous studies conducted on domestic birds, and more recently on wild birds (Lynn, In press). The first evidence of the role of prolactin in the regulation of parental behavior came from the studies of Riddle that demonstrated the functional link between increased circulating prolactin levels and the development of the crop gland that serves to feed young chicks in pigeons (Riddle et al., 1935; Goldsmith et al., 1981; Lea et al., 1991). In this section, we aim to review evidence of the functional link between prolactin and parental behavior in birds.

Prolactin secretion and reproductive modes

Following the studies by Riddle, further evidence came from the simultaneous increase in both circulating prolactin levels and the expression of incubation behavior. In birds, prolactin secretion increases with lengthening day at the onset of the breeding season (Hall et al., 1986; Dawson and Sharp, 1998; Dawson et al., 2001). Independently of this effect of photoperiod on prolactin levels, prolactin secretion is dramatically accentuated when individuals enter into the parental phase (Dawson and Goldsmith, 1985) and elevated prolactin levels are maintained in parent birds through visual and contact stimuli from the egg, the chick(s), the nest or even the mate (Silver, 1984; Hall et al., 1986; Hall, 1987; Leboucher et al., 1993; Sharp et al., 1998). Importantly, all bird species do not seem to follow the same pattern of prolactin secretion (Fig. 2A). Although all species exhibit elevated circulating prolactin levels during incubation, prolactin levels drop at the time of hatching in many precocial species (Fig. 2A, Etches et al., 1979; Sharp et al., 1979; Lea et al., 1981; Goldsmith and Williams, 1980; Goldsmith, 1982; Hall and Goldsmith, 1983) whereas they remain elevated during the chick-

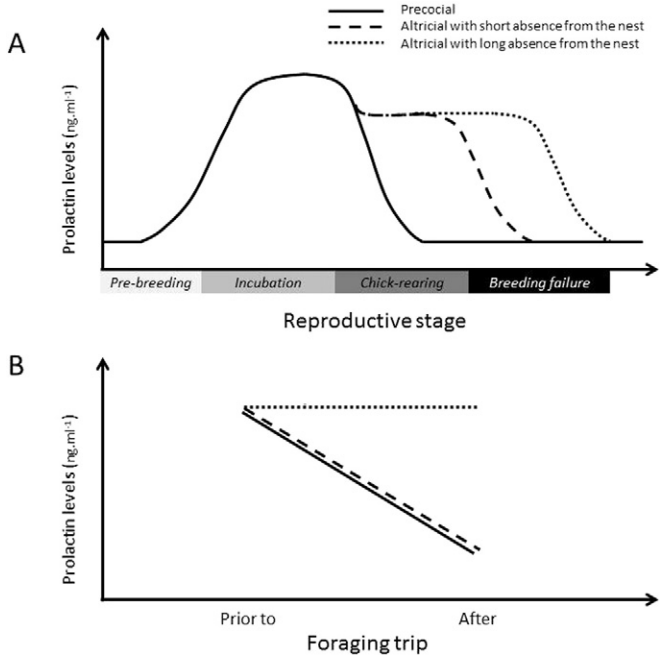

Fig. 2. A. A schematic representation of the prolactin cycle of breeding birds with different reproductive modes (precocial such as fowls, ducks and geese; altricial with short absence from the nest such as gannets, starlings, and doves; altricial with long absence from the nest such as penguins, albatrosses and petrels). B. A schematic representation of the influence of the absence from the nest on prolactin levels for incubating birds with different reproductive modes (precocial, altricial with short absence from the nest, and altricial with long absence from the nest).

rearing period in altricial species (Fig. 2A, Dawson and Goldsmith, 1982; Hector and Goldsmith, 1985; Hall, 1986; Seiler et al., 1992; Lormée et al., 1999, 2000; Vleck et al., 2000; Riou et al., 2010; Angelier et al., 2013). Similarly, prolactin levels of males and females appear tightly linked to their role in providing parental cares (Buntin, 1996; Van Roo et al., 2003). Prolactin levels in female are higher than those of the male when the female provides more parental care. On the other hand, this pattern is reversed when the male provides more parental care than the female (Oring et al., 1988; Gratto-Trevor et al., 1990). These patterns strongly suggest that elevated prolactin levels are necessary to maintain the intense parental effort (brooding and feeding) of chick-rearing birds in altricial species. However, this maintenance of elevated prolactin levels during the chick-rearing period in altricial species could also result from high visual and contact stimuli from the chicks or the nest that are not as present in precocial species (Sharp et al., 1998).

To disentangle the relative importance of these two hypotheses, useful insights come from the prolactin cycle of particular seabird species. Among altricial species, penguins, petrels and albatrosses have an extreme breeding cycle: during the incubation and chick-rearing phases, parents take turns and fast at the nest to incubate their egg or guard their chick while their mate is at sea to restore its body condition. These foraging trips can last several days or even weeks. Despite the absence of visual or contact stimuli from the egg, the nest or the mate, elevated prolactin levels are maintained during these trips in these species (Fig. 2B; Hector and Goldsmith, 1985; Garcia et al., 1996; Lormée et al., 1999; Vleck et al., 2000) and parents resume their parental duties when back at the nest. Moreover, and contrary to many other precocial or altricial species (e.g. Hall, 1986), elevated prolactin levels are maintained in these particular seabird species even if breeding failure occurs (loss of the egg or the chick, e.g. Jouventin and Mauget (1996); Fig. 2A). These findings demonstrate therefore that all these visual or contact stimuli are not absolutely required to maintain elevated prolactin levels in chick-rearing birds. As a conclusion, the study of these three different reproductive modes (precocial, altricial, and 'extreme' altricial) suggests that prolactin secretion may be more tightly linked to the necessity to provide important parental behavior to the chicks (e.g. feeding and nest attendance) than to the stimuli from the chick in chick-rearing birds.

Prolactin and parental behavior in domestic birds

Domestic animal studies have provided strong evidence that prolactin plays a major role in the initiation and the maintenance of incubation behavior in birds. Experimental increases in prolactin levels induce the onset of incubation behavior in turkey hens (Youngren et al., 1991). Moreover, immunization against prolactin or vasoactive-intestinal peptide (VIP) – a hypothalamic releaser of prolactin secretion – resulted in turkey and chicken hens failing to engage in incubation behavior (El Halawani et al., 1995, 1996; Crisostomo et al., 1998; Li et al., 2011). Although these findings demonstrate that prolactin is essential to the onset of incubation, elevated prolactin levels and stimuli from the egg do not appear sufficient to induce incubation behavior under some circumstances (Lehrman, 1963; Silver, 1984; Buntin and Tesch, 1985). Actually, prolactin appears unable to stimulate the onset of incubation without a previous increase in progesterone and estradiol levels (El Halawani et al., 1986; El Halawani and Rozenboim, 1993). Overall, elevated prolactin levels appear necessary for incubation readiness, but additionally this hormone interacts with others to initiate the beginning of the parental phase (El Halawani et al., 1986).

Once incubation has started, there is a clear connection between prolactin secretion, stimulation of the brood patch by the contact with the egg, and incubation behavior (Sharp et al., 1998). Prolactin secretion drops dramatically when the brood patch is anesthetized in turkey hens and domestic ducks (Hall and Goldsmith, 1983; Book, 1991), and additionally, female turkey hens do not display any incubation behavior when their brood patch is denervated (Book, 1991). At the ultimate level, this interplay between prolactin, incubation-related stimuli and parental behavior may allow individuals to adjust their parental behavior to their current breeding status. Interestingly, parent birds usually stop incubating their egg after a specific duration if it does not hatch and this termination of incubation is preceded by a decline in prolactin levels. This finding supports the idea that prolactin is linked to incubation behavior (Silver and Gibson, 1980). Several studies also experimentally demonstrated that the duration of incubation can be extended by artificially increasing prolactin levels of incubating doves (Lea et al., 1986; Lea and Sharp, 1991). Moreover, experimental injection of prolactin restored incubation behavior in doves that were isolated from their nest and egg for several days (Janik and Buntin, 1985), and similarly, experimental injections of prolactin maintain the motivation to incubate in nest-deprived bantam hens (Sharp et al., 1988). All these studies clearly demonstrate the functional role of prolactin secretion in facilitating and maintaining incubation behavior (Silver, 1984; Sharp et al., 1988, 1998).

Regarding the chick-rearing period, there is also strong evidence that prolactin facilitates multiple parental behaviors. For instance, experimentally increased prolactin levels are associated with a higher frequency of regurgitation to feed the chick and a higher motivation to protect the chick in ring doves (Buntin et al., 1991; Wang and Buntin, 1999). Supporting even further the role of prolactin in stimulating parental behavior, a few studies reported that experimental manipulations of circulating prolactin levels were associated with the expression of parental behavior in non-breeder ring doves (Lehrman, 1955; Slawski and Buntin, 1985). Interestingly, the contact of a parent with a hungry chick is associated with a release of prolactin levels in doves (Buntin, 1979). Since prolactin seems to facilitate regurgitation and chick feeding in this species (Wang and Buntin, 1999), this result suggests that the regulation of prolactin levels may orchestrate the parental response to chick demands.

Prolactin and parental behavior in wild birds

Most of our knowledge on the role of prolactin on parental behavior comes from domestic animals and the influence of prolactin levels on parental behavior in wild species has been far less studied. Pedersen (1989) found that an experimental increase in prolactin levels in ptarmigans, *Lagopus lagopus*, did not dramatically modify incubation behavior although they seemed to exhibit better incubation assiduity than controls. Sockman et al. (2000) found that a moderate experimental increase in prolactin levels results in a better incubation assiduity in American kestrels, *Falco sparvius*, although the injection of the highest prolactin dose did not trigger this behavioral change. Several studies also showed that low prolactin levels are clearly correlated with the decision to stop incubation duties and to abandon the egg (Cherel et al., 1994; Groscolas et al., 2008; Spée et al., 2010; Angelier et al., 2007a, 2015). More recently, Thierry et al. (2013) experimentally demonstrated that a reduction of prolactin levels is associated with a modification of the incubation behavior in Adélie penguins, leading to a lower quality of incubation and a higher risk of egg predation. Although limited in number, these studies clearly show that the findings on domestic birds also apply to wild ones.

Prolactin also seems to facilitate parental behavior during the chick-rearing period in wild birds. For example, prolactin-treated ptarmigans had shorter flushing distance when disturbed at the nest and appeared more protective towards their chicks than controls (Pedersen, 1989). Several studies also found that prolactin and the expression of alloparental behaviors are correlated in cooperative breeders (Vleck et al., 1991; Schoech et al., 1996; Khan et al., 2001) and an experimental reduction of prolactin levels is even associated with a reduction of alloparental behaviors in the Emperor penguin, *Aptenodytes fosteri* (Angelier et al., 2006a). In some studies, prolactin levels were positively correlated with the expression of parental behavior, such as chick provisioning (Duckworth et al., 2003; Boos et al., 2007). Supporting the functional role of prolactin in mediating parental behavior, experimental decrease and increase of prolactin levels respectively reduce and promote brood provisioning in House finches (Badayev and Duckworth,

2005). Finally, Angelier et al. (2009a) showed that reduced prolactin levels were associated with a lower nest attendance and a lower motivation to come back to the nest after a disturbance in chick-rearing black-legged kittiwakes (*Rissa tridactyla*).

Future directions

Despite the clear causal relationships between prolactin levels and parental behavior, they appear disconnected under several circumstances (reviewed in Williams (2012)). For instance, incubation starts in doves and pigeons before prolactin levels begin to rise (Silver, 1984) and prolactin levels are not correlated with parental provisioning or brood defense behavior in several studies (Ketterson et al., 1990; Silverin and Goldsmith, 1984; Kosztolanyi et al., 2012; Wojczulanis-Jakubas et al., 2013). Another striking example highlighted by Williams (2012) is the prolactin cycle of the brood parasitic brown-headed cowbird: Despite the absence of incubation behavior and parental provisioning, prolactin levels increase in this species in the same way as many other species that provide intense parental care (Dufty et al., 1987). Do all these examples mean that prolactin is not as tightly linked to parental behavior as previously thought?

Several explanations can be proposed to explain these discrepancies and they need to be appropriately tested in future studies. First, prolactin levels could change independently of parental care in some species. Prolactin is well-known as being a pleiotropic hormone with multiple actions that are not developed in depth in this review (metabolic, osmoregulation, etc.) and circulating prolactin levels can also change in respect to multiple factors that are not linked to parental behavior, such as day length, time of the day or metabolic needs (Meier et al., 1969; Hall et al., 1986; Dawson, 2006; Holberton et al., 2008). Therefore, observed changes in prolactin levels may not always be related to changes in the expression of parental cares, as suggested by Dufty et al. (1987). Second, the influence of prolactin on parental behavior may not only depend on circulating prolactin levels but also on the location and density of prolactin receptors. This could explain why expression of parental behavior is not correlated with prolactin under all circumstances (e.g. Dufty et al., 1987). Supporting this idea, the effect of prolactin injection on parental behavior varies greatly between experienced and non-experienced individuals in ring doves (Wang and Buntin, 1999). Similarly, a difference in prolactin regulation between inexperienced and experienced breeders has been reported in zebra finches (Christensen and Vleck, 2008). These findings suggest that measuring circulating prolactin levels may not always be sufficient to assess the motivation to provide parental cares in birds. Third, prolactin may act with other hormones to mediate changes in parental behavior. Under some situations, variations in prolactin levels could be the main driver of changes in the expression of parental behaviors whereas it may be the case of other hormones in other situations. Supporting this theory, two studies found that testosterone injections reduce parental care without affecting prolactin levels in Dark-eyed juncos, *Junco hyemalis*, and spotted sandpipers, *Actitis maecularia* (Oring et al., 1989; Schoech et al., 1998). Finally, there is growing evidence that the relationship between parental care and circulating prolactin levels is complex and non-linear. Indeed, changes in parental behavior seem to occur only when prolactin levels reach a lower threshold (Boos et al., 2007; Angelier and Chastel, 2009; Spée et al., 2010). Above this threshold that may be determined by receptor densities and locations, elevated prolactin levels may only have a permissive effect on parental behavior and variations in the expression of parental behavior could be mediated by other endocrine mechanisms.

Stress, breeding success and prolactin

Environmental conditions and prolactin levels

We are currently lacking data on the effect of environmental conditions and circulating prolactin levels in wild birds. To our knowledge, only three studies have examined the relationship between circulating prolactin and environmental conditions in parent birds. First, Riechert et al. (2014a) found that prolactin levels were not correlated with food abundance in Common terns although prolactin titers were particularly low during two years of low food availability. Second, Leclaire et al. (2011) found that prolactin levels were not affected by an experimental handicap (i.e. clipping of a few flight feathers) that aimed to increase foraging costs in black-legged kittiwake parents. Third, Delehanty et al. (1997) reported that, independently of clutch size, prolactin levels of incubating phalaropes were reduced during a year of severe drought, and body mass loss was responsible for these low prolactin levels (Delehanty et al., 1997). Although the result on kittiwakes was inconclusive, the two other studies suggest that energetic condition and circulating prolactin levels could be functionally linked.

The influence of fasting or dietary constraints on the circulating prolactin levels of parents has rarely been examined in domestic birds, and surprisingly, most information comes from wild birds. To our knowledge, a single study has examined this question in domestic birds and it did not report any correlation between prolactin levels and the energetic status of chicken hens (Zadworny et al., 1988). Although this result was confirmed in several studies on wild birds (Hector and Goldsmith, 1985; Cherel et al., 1994; Angelier et al., 2009b, 2013, 2015; Heidinger et al., 2010; Kosztolanyi et al., 2012; Crossin et al., 2012), others found that parent birds have lower prolactin levels when in poor body condition (Criscuolo et al., 2006; Jonsson et al., 2006; O'Dwyer et al., 2006; Angelier et al., 2007b, 2009b; Groscolas et al., 2008; Spée et al., 2010; Schmid et al., 2011; Riechert et al., 2014b). The negative impact of nutritional conditions on circulating prolactin levels seems to only appear when individuals reach a lower threshold of body condition. Thus, Cherel et al. (1994) clearly report that long-term fasting, but not short-term fasting, was associated with a sharp and rapid fall of prolactin levels in king penguins. This finding was then confirmed in a few other species (Criscuolo et al., 2002; Groscolas et al., 2008; Spée et al., 2010). Supporting the idea of a non-linear relationship between prolactin levels and the energetic status, the negative relationship between prolactin levels and body condition becomes more apparent as individuals are more energetically constrained (O'Dwyer et al., 2006; Angelier et al., 2009b; Riechert et al., 2014b).

So far and surprisingly, most studies have focused on seabirds that are characterized by large body reserves (i.e. capital breeders). The relationship between circulating prolactin levels and the energetic status could be different in smaller species that does not rely on large amount of body reserves. Because these birds cannot rely on their body reserves for an extended period of time in case of reduced food availability, we could expect prolactin levels to be more sensitive to environmental constraints. To better understand the functional link between prolactin levels and environmental conditions, future studies should therefore examine the impact of further environmental constraints on prolactin levels in parents of bird species with contrasted life-history strategies.

Prolactin and breeding success

There is increasing evidence that prolactin levels can be related to reproductive performances in wild parent birds. For instance, Riechert et al. (2014a) recently reported a significant and positive correlation between breeding success and prolactin levels in Common terns. Low prolactin levels were also associated with breeding failure in snow petrels (*Pagodroma nivea*) and cape petrels (*Daption capense*, Angelier et al., 2013, 2015). Miller et al. (2009) found that baseline prolactin levels were positively correlated with nestling weight in mourning doves (*Zenaida macroura*), suggesting therefore that elevated prolactin levels may increase breeding success by promoting parental care (i.e. feeding). Finally, Cavanaugh et al. (1983) also found that contamination by petroleum resulted in both lower prolactin levels and lower breeding success in mallards. Since prolactin levels are known to depend on stimuli from the eggs or the chicks, these positive relationships between prolactin

levels and breeding success could result from strong stimuli from the egg or the chick in successful breeders (e.g. larger clutch or brood size, and higher nest attendance). Alternatively, it could result from a direct functional effect of prolactin levels on the quality of parental behavior and therefore breeding success. Supporting this later hypothesis, a decline in prolactin levels seems to precede the decision to abandon the nest in several studies (Silver and Gibson, 1980; Chastel and Lormée, 2002; Angelier et al., 2007a, 2015). This hypothesis is also supported by a few experimental studies that have investigated the influence of manipulated prolactin levels on reproductive performances. For example, an experimental increase in prolactin levels is associated with a better breeding success in ptarmigans as a result of a higher risk-taking strategy in terms of brood defense behavior (Pedersen, 1989). Experimentally reduced prolactin levels also resulted in a lower breeding success in incubating Adélie penguins and chick-rearing black-legged kittiwakes (Angelier et al., 2009a; Thierry et al., 2013). Additional support for a functional relationship between reproductive performances and prolactin levels comes from indirect data. Inexperienced parents are known to be in poorer condition and to reproduce less well than experienced ones and they concomitantly show reduced prolactin levels (Deviche et al., 2000; Préault et al., 2005; Angelier et al., 2006b, 2007b; Riechert et al., 2012), supporting therefore the idea that environmental conditions, prolactin levels and breeding success are connected.

On the other hand, several studies did not report any relationship between breeding success and prolactin levels (Angelier et al., 2007b; Schmid et al., 2011; Kosztolanyi et al., 2012; Cottin et al., 2014). Although prolactin is thought to affect reproductive performances through its action on parental behavior, the relationship between parental behavior and circulating prolactin levels appears complex and non-linear. Therefore, it is not very surprising that the link between breeding success and prolactin levels is somewhat inconsistent. Several causes can be proposed to explain this inconsistency. First, breeding failure could be relatively independent of parental behavior and may be more related to chance in some species (Kosztolanyi et al., 2012). Second, some aspects of parental behavior may be under control of other endocrine pathways. Although a decrease in prolactin levels could trigger a reduction of parental effort, variations in parental effort may for example be under control of other hormones when prolactin levels remain above an upper threshold (e.g. corticosterone: Bonier et al., 2009; testosterone: Wingfield et al., 1990). Third, breeding success often depends on both parents in birds and most correlations between prolactin levels and breeding success come from one parent and are probably not a good proxy of the effort of its mate. Because of the limited number of studies that have linked prolactin levels and breeding success, we suggest that future correlative and experimental studies should examine this link. They should also look at multiple endocrine mechanisms not only to compare their relative importance in predicting breeding success, but also to understand whether they interact to affect breeding success.

The prolactin stress response in parent birds

As stated previously, there seems to be a connection between reduced prolactin levels and environmental or nutritional constraints. In addition, a few early studies also suggested that an acute stressor can trigger such a reduction of prolactin levels in parent birds. Opel and Proudman (1986) found that prolactin levels decrease in response to capture and restraint in incubating turkeys. Maney et al. (1999a) reported that prolactin levels decrease in response to handling stress in incubating Florida scrub jays. More recently, this pattern has been confirmed in many wild species (Table 1) by using a standardized stress protocol classically used to measure the adrenocortical stress response (Wingfield et al., 1992). This protocol consists of measuring the change in circulating prolactin levels in response to a capture and a 30 min handling stress. During restraint stress, parents are removed from the nest and there is therefore not any contact between the nest, the eggs or the chicks and the parent. Since these stimuli are necessary to maintain prolactin secretion in most species (Sharp et al., 1988), the observed decrease in prolactin levels could result from the absence of these stimuli rather than from the stress itself. A few studies suggest that stress functionally affects prolactin levels independently of these stimuli: low prolactin levels can be associated with environmental stressors independently of restraint (drought: Delehanty et al., 1997; low food availability: Riechert et al., 2014a) and, in some species, prolactin levels decrease in response to stress in non-breeders or failed breeders that are not engaged into parental activities (Chastel et al., 2005; Riou et al., 2010; Angelier et al., 2015). Future studies are however required to fully demonstrate that a stressor can affect prolactin levels independently of breeding activity.

This restraint stress protocol has allowed endocrinologists to compare the prolactin stress response among individuals and species (Angelier et al., 2013) and it has demonstrated that a stress-induced decrease in prolactin levels varies greatly between individuals (see Kosztolanyi et al. (2012) for an example), but also among species (Table 1). Some individuals maintain elevated prolactin levels in response to this standardized stress protocol whereas others show a drastic drop in prolactin levels. Similarly, most species exhibit a drop in circulating prolactin levels in response to this protocol but a few others seem to be able to maintain or even to slightly increase their circulating prolactin levels in response to stress (Table 1). From a life-history perspective, this inter-individual and inter-species variation in the prolactin stress response is promising because it may be associated with variations in life-history decisions and strategies (Angelier and Chastel, 2009). Because prolactin seems to facilitate parental behavior, a sharp decline in response to a standardized stressor suggests that the parent will be prone to reduce parental effort in the face of environmental constraints (Fig. 3). This may translate into a lower incubation assiduity, a lower brooding/provisioning commitment or ultimately into egg or brood desertion (see the Prolactin and parental behavior section). On the other hand, the maintenance of prolactin levels in response to a standardized stress protocol suggests that the parent will maintain parental behaviors despite environmental constraints (Fig. 3). This may be associated with a high risk-taking strategy since parental effort may be then associated with important nutritional constraints and a higher risk of predation, which may compromise the parent's survival. Instead of the prolactin stress response, the corticosterone stress response has classically been used to investigate parental investment in birds (Wingfield et al., 1998; Wingfield and Sapolsky, 2003). Thus, it has been shown that the corticosterone stress response varies among individuals (Lendvai et al., 2007; Goutte et al., 2010), populations (Silverin et al., 1997; Breuner et al., 2003) and species (Bokony et al., 2009; Hau et al., 2010) and these differences can be related to specific parental decisions and life-history strategies (Wingfield and Sapolsky, 2003; Angelier and Wingfield, 2013). Although the corticosterone and the prolactin stress responses have rarely been examined together, they often provide complementary information on parental investment in parent birds (Chastel et al., 2005; Angelier et al., 2007a, 2009b, 2013, 2015; Heidinger et al., 2006, 2010; Schmid et al., 2011, 2013). For instance, the corticosterone stress response was not related to parental decisions in a recent study of incubating snow petrels, but it was tightly correlated to the energetic status of the parents. On the other hand, the prolactin stress response was a reliable predictor of the decision to abandon the egg, but it was not correlated with the energetic status of the parents (Angelier et al., 2015).

Supporting the hypothesis that the corticosterone and the prolactin stress responses provide different information on parental investment in birds, prolactin and corticosterone levels are rarely correlated in parent birds (reviewed in Angelier et al. (2013)). Corticosterone seems to affect prolactin secretion, but only when corticosterone levels reach very high levels during a few days (Criscuolo et al., 2005; Angelier et al., 2009a; Spée et al., 2011). In turn, prolactin seems to respectively facilitate or inhibit corticosterone secretion depending on the situation (Koch et al., 2004; Cottin et al., 2014). Moreover, prolactin and

Table 1
Review of the existing studies that examined the influence of a stressor on prolactin levels in domestic and wild birds. The signs '−', '+' respectively mean that prolactin levels significantly decrease or increase in response to the stressor. The sign '=' means that prolactin levels did not significantly change in response to the stressor.

Species	Domestic/wild	Captivity	Breeding stage	Stressor	Change in prolactin levels	Reference
Turkey	Domestic	Captive	Incubating	Repeated handling	−	Opel and Proudman (1986)
Turkey	Domestic	Captive	Pre-breeding	Repeated handling	+	Opel and Proudman (1986)
Turkey	Domestic	Captive	Non-breeding	Repeated handling	+	Opel and Proudman (1986)
Turkey	Domestic	Captive	Non-breeding	Handling stress	+	El Halawani et al. (1985)
Chicken	Domestic	Captive	Non-breeding	Cold stress	+	Harvey et al. (1977)
Chicken	Domestic	Captive	Non-breeding	Heat stress	=	Harvey et al. (1977)
Semi palmated Sandpiper	Wild	Free-living	Incubating	Handling stress	−	Gratto-Trevor et al. (1991)
Florida Srub Jay	Wild	Free-living	Incubating	Handling stress (15 min)	−	Maney et al. (1999a,b)
Darked eyed-Junco	Wild	Captive	Pre-breeding	Handling stress (20 min)	=	Maney et al. (1999a,b)
White-crowned Sparrow	Wild	Captive	Non-breeding	Handling stress (20 min)	=	Maney et al. (1999a,b)
Western Scrub Jay	Wild	Captive	Non-breeding	Handling stress (30 min)	=	Maney et al. (1999a,b)
Back-legged Kittiwake	Wild	Free-living	Chick rearing	Handling stress (30 min)	=	Chastel et al. (2005)
Back-legged Kittiwake	Wild	Free-living	Failed breeders	Handling stress (30 min)	−	Chastel et al. (2005)
Back-legged Kittiwake	Wild	Free-living	Chick rearing	Handling stress (30 min)	=	Leclaire et al. (2011)
Snow Petrel	Wild	Free-living	Incubating	Handling stress (30 min)	−	Angelier et al. (2007a,b)
Snow Petrel	Wild	Free-living	Incubating	Handling stress (30 min)	−	Angelier et al. (2009a,b)
Snow Petrel	Wild	Free-living	Chick-rearing	Handling stress (30 min)	−	Angelier et al. (2009a,b)
Snow Petrel	Wild	Free-living	Failed breeders	Handling stress (30 min)	−	Angelier et al. (2009a,b)
Cape Petrel	Wild	Free-living	Incubating	Handling stress (30 min)	−	Angelier et al. (2013)
Cape Petrel	Wild	Free-living	chick-rearing	Handling stress (30 min)	−	Angelier et al. (2013)
Cape Petrel	Wild	Free-living	Failed breeders	Handling stress (30 min)	+	Angelier et al. (2013)
Glaucous gull	Wild	Free-living	Incubating	Handling stress (30 min)	−	Verreault et al. (2008)
Mourning dove	Wild	Free-living	Chick-rearing	handling stress (30 min)	=	Miller et al. (2009)
Common Tern	Wild	Free-living	Incubating	Handling stress (30 min)	−	Heidinger et al. (2010)
Manx Shearwater	Wild	Free-living	Pre-breeding	handling stress (30 min)	+	Riou et al. (2010)
Manx Shearwater	Wild	Free-living	Incubating	Handling stress (30 min)	−	Riou et al. (2010)
Manx Shearwater	Wild	Free-living	Early chick-rearing	handling stress (15 min)	−	Riou et al. (2010)
Manx Shearwater	Wild	Free-living	Late chick-rearing	Handling stress (30 min)	+	Riou et al. (2010)
Manx Shearwater	Wild	Free-living	Failed breeders	Handling stress (30 min)	+	Riou et al. (2010)
Manx Shearwater	Wild	Free-living	Non-breeding	Handling stress (30 min)	+	Riou et al. (2010)
Eurasian hoopoe	Wild	Free-living	Chick-rearing	Handling stress (30 min)	−	Schmid et al. (2011)
Kentish plover	Wild	Free-living	Chick-rearing	Handling stress (30 min)	−	Kosztolanyi et al. (2012)
Little auk	Wild	Free-living	Chick-rearing	Handling stress (30 min)	+	Wojczulanis-Jakubas et al. (2013)

corticosterone do not follow the same kinetic in response to a standardized stress protocol. A recent study has for instance emphasized that the corticosterone and prolactin stress recoveries are very different in parent seabirds. When the stressor ends, corticosterone levels return quite quickly to baseline pre-stress levels whereas prolactin levels remain low for a much longer duration (Angelier et al., 2015). All these results support the idea that prolactin and corticosterone do not mediate the same response to stress and that they probably interact to maintain homeostasis in parent birds. Indeed, moderately elevated corticosterone levels are known to facilitate reproduction through metabolic and foraging adjustments (Bonier et al., 2009; Love et al., 2014) whereas prolactin may be more tightly linked to parental behavior per se (Hall et al., 1986; Buntin, 1996; Vleck, 1998; Sockman et al., 2006; Angelier and Chastel, 2009). Although this hypothesis has never been tested, the effect of one hormone might also depend on the level of the other hormone and elevated corticosterone levels might have different behavioral and physiological effects depending on circulating prolactin levels. Only a few studies have investigated the effect of the individual state or environmental conditions on both corticosterone and prolactin stress responses and we currently lack descriptive data not only on the kinetics of these two responses but also on their functional link. Therefore, future field and laboratory studies should also aim to better understand the respective role of corticosterone and prolactin in mediating the parental response to a stressor.

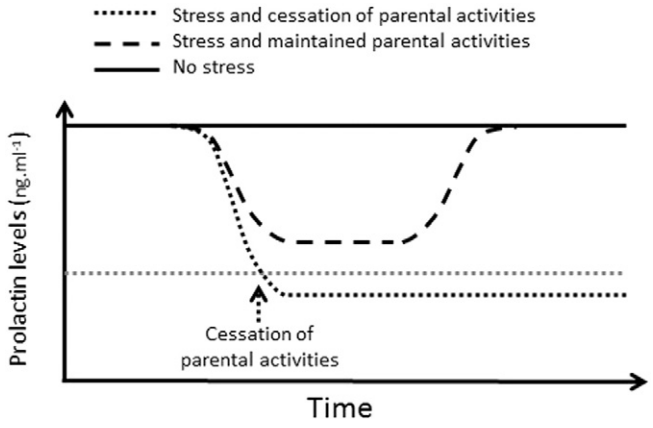

Fig. 3. A schematic representation of changes in prolactin levels in response to stress during the parental phase. The solid line represents a situation without stressor: Prolactin levels remain elevated and parental behavior is maintained. The dotted line represents a situation of stress with reduced parental investment: Prolactin levels are dramatically reduced, fall below a threshold (dotted gray line) and this is associated with a cessation of parental activities (dotted arrow) and with the end of the parental phase. The dashed line represents a situation of stress with maintained parental investment: Prolactin levels decrease but they did not reach the lower threshold. This resistance to stress is associated with the maintenance of parental behavior that is only slightly reduced (see also Angelier and Chastel (2009)).

Prolactin and endocrine disruption in parent birds

Given its key role in mediating parental investment in birds, any disruption of prolactin, dopamine, or vasoactive intestinal peptide secretion would alter the ability of an individual to adjust parental behavior to environmental conditions. Such a disruption may originate from exposure to environmental contaminants such as heavy metals (mercury, cadmium), persistent organic pollutants (POPs: organochlorine pesticides (OCP), polychlorinated biphenyls (PCB), brominated flame retardants, poly- and perfluorinated alkyl substances (PFAS), or polycyclic aromatic hydrocarbons (PAH)). Despite the well-established endocrine disruptive properties of these contaminants (e.g. Tyler et al., 1998; Tan et al., 2009), only a handful of studies have examined relationships between avian prolactin secretion and environmental contaminants. The first investigations came from captive mallards (*Anas platyrhynchos*)

studies showing that petroleum ingestion resulted in a decrease in prolactin levels (Cavanaugh et al., 1983; Harvey et al., 1981). In contrast, in another study of mallards exposed to cadmium, no effect on plasma prolactin levels was observed (Hughes et al., 2003). Regarding POPs, it has been shown that experimentally PCB-exposed male American kestrels (*Falco sparverius*) showed a significant reduction in the size of their brood patch (Fisher et al., 2006), which is in part under prolactin control (Buntin, 1996). However, in this study prolactin concentrations were not assayed, and thus no link between PCB and prolactin could be established.

The first study on free-ranging birds was conducted on incubating glaucous gulls (*Larus hyperboreus*), a top predator in the Norwegian Arctic, and which accumulates some of the highest burden of POPs among any Arctic seabirds (Verreault et al., 2008). It was found that baseline and stress-induced prolactin levels tended to vary negatively with plasma concentration of OCP, PCB, brominated flame retardants, and associated metabolic products in males, but not in females. However, given the complex cocktail of POPs and associated metabolic products that was included in the analysis, it is difficult to determine which compound was precisely involved in these relationships. A recent study on another free-living seabird, the snow petrel, has investigated the respective influences of OCP, PCB and mercury on prolactin secretion (Tartu et al., 2015): in incubating males, stress-induced prolactin levels significantly decreased with increasing mercury whereas no relationship was found between prolactin levels and POPs. However, POPs were significantly related to stress hormones. This study suggested that POPs and mercury could be related to different hormonal pathways; POPs may disrupt the HPA axis whereas mercury would impair prolactin and more generally pituitary hormone secretion (Tartu et al., 2013, 2015). Similar associations between mercury levels and prolactin secretion have been found in males of two other seabird species (black-legged kittiwakes and magnificent frigatebird *Fregata magnificens*; Tartu et al. unpublished, Chastel et al. unpublished). To confirm the potential important role of mercury in avian prolactin disruption, more studies including experimental supports are needed. Future studies should also focus on the possible mechanisms involved to determine how prolactin release can be affected by the direct or indirect modulating actions of contaminants. Contaminants may interfere with enzymes involved in steroidogenesis [e.g., hydroxysteroid dehydrogenase (HSD) and cytochrome P450 (CYP) enzymes], or less directly through modulation of the feedback mechanisms in the hypothalamus–pituitary–gonadal axis (Sanderson and van den Berg, 2003). Environmental contaminants may also directly alter prolactin secretion through a chemically-induced dysregulation of dopamine neurotransmitters that are involved in the modulation of PRL secretion, as demonstrated in laboratory rodents (Faro et al., 2007; Lafuente et al., 2000).

Stress, prolactin, clutch size and molt

Stage-dependent prolactin stress response

Interestingly, the prolactin stress response is not always characterized by a reduction of prolactin levels (Table 1). As in mammals, circulating prolactin levels have classically been reported to increase in response to stress in early studies of birds (Hall et al., 1986; Scanes and Harvey, 1981). For instance, prolactin levels increase in response to cold or immobilization stress in domestic birds (Harvey et al., 1977, 1978; Opel and Proudman, 1986) and the stress of a high parasite load or an infection results in increased prolactin levels in domestic fowls (Chadwick et al., 1985; Davison et al., 1985). Interestingly, Opel and Proudman (1986) reported that prolactin levels respectively increase and decrease in non-breeding and incubating turkeys, suggesting that the prolactin stress response differs dramatically between non-breeders and parents. Supporting these earlier studies on domestic birds, two recent studies also reported that prolactin levels can increase in response to stress when parents are not providing intense parental cares (Riou et al., 2010; Angelier et al., 2013). For example, Riou et al. (2010) found that prolactin levels increase in response to a standardized stress protocol in Manx shearwaters during the pre-breeding period and they found the same patterns towards the end of the chick-rearing period. In failed breeders, the same pattern was found in Cape petrels and Manx shearwaters (Riou et al., 2010; Angelier et al., 2013) but not in black-legged kittiwakes and snow petrels (Chastel et al., 2005; Angelier et al., 2009b). The causes of this discrepancy are not known but snow petrels and kittiwakes may have been sampled too soon after their breeding failure.

There seems to be a strong effect of the breeding stage on the prolactin stress response in birds (Table 1). In pre-laying and failed breeders, prolactin levels are much lower than in parents and prolactin is likely to have totally different effects on physiology and behavior. This means that the prolactin stress response may mediate other life-history decisions. We obviously lack data about the prolactin stress response in birds that are not engaged in parental activities, but Opel and Proudman (1986) reported that habituation can reduce the stress-induced increase in prolactin levels in non-breeding hens. This suggests that the prolactin stress response can also be modulated according to environmental conditions in non-parent birds. In the following paragraphs, we raise hypotheses regarding the functional role of this prolactin stress response in pre-breeding and molting birds.

Prolactin, stress and clutch size determination

The reproductive function of prolactin is certainly not limited to the regulation of parental behaviors. Prolactin is also thought to govern the transition from the pre-breeding stage to the parental phase, and therefore, to determine the timing of egg-laying and the clutch size (Sockman et al., 2006). Classically, circulating prolactin levels remain very low during most of the annual cycle of birds (Silverin et al., 1989), and then, increase as individuals engage into reproductive activities and as females lay their eggs (Hall, 1986; Sockman et al., 2006). This increase is primarily the result of increased photoperiod (Dawson et al., 2001) and, then, from contact and/or visual stimuli with the egg that are known to stimulate prolactin secretion in many bird species (Dawson and Goldsmith, 1985; Sharp et al., 1998). In turn, elevated prolactin levels are known to simultaneously increase the motivation of both parents to engage in incubating activities, and concomitantly, inhibit the endocrine axis related to egg production and laying. Prolactin is known to have anti-steroidogenic effects and prolactin levels are usually negatively correlated with progesterone, testosterone, and luteinizing hormone (LH) levels (Hall, 1986; Dawson and Sharp, 1998). In addition, an experimental increase of prolactin levels triggers a reduction of gonadotropin releasing hormone (GnRH) in vivo and in vitro (El Halawani et al., 1991; Rozenboim et al., 1993; You et al., 1995). Finally, experimental studies have shown that elevated prolactin levels induce incubation activities, reduce gonadal weight and suppress egg laying (Buntin and Tesch, 1985; Youngren et al., 1991; Rozenboim et al., 2004; but see Williams (2012); Ryan et al. (2014)). For all these reasons, this increase in prolactin levels is thought to lead to the transition from the egg-laying phase to the parental phase and it may therefore determine the clutch size (Sockman et al., 2006; Fig. 4A). Although this theory has been tested and supported by a few studies (Youngren et al., 1991; El Halawani et al., 1996; Crisostomo et al., 1998; Sockman et al., 2000; Ouyang et al., 2011; but see Williams, 2012; Ryan et al., 2014, 2015), the influence of stressors on prolactin levels has not been integrated into this theory. To the best of our knowledge, the combined influence of stress on prolactin levels and laying effort has rarely been investigated (but see Rozenboim et al. (2004)). Contrary to the parental phase, stress is associated with an increase in circulating prolactin levels in pre-breeding birds (see the Stage-dependent prolactin stress response section). Because elevated prolactin levels are thought to stimulate the termination of egg laying, a stress-related increase in prolactin levels could accelerate this phenomenon, and therefore, control for clutch size

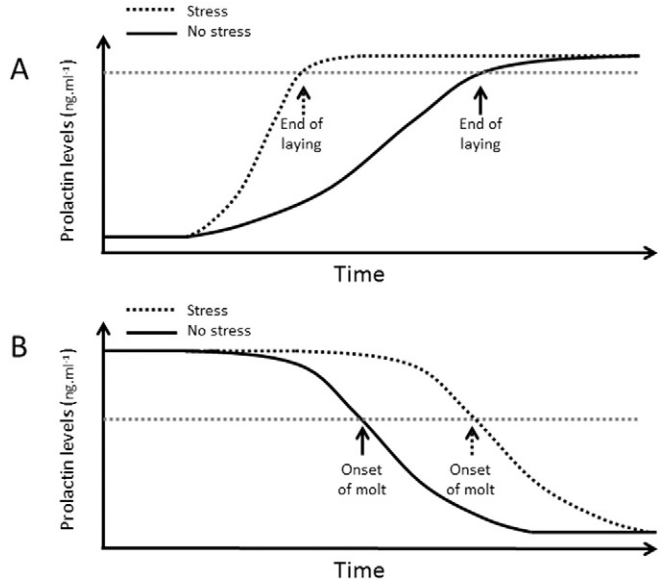

Fig. 4. A. A schematic representation of changes in prolactin levels in response to stress during the laying phase. The solid black line represents a situation without stressor: Prolactin levels increase through the laying and laying stops (black solid arrow) when prolactin levels reach an upper threshold (gray dotted line). The rate of this increase determines therefore the clutch size (see also Sockman et al. (2006)). The black dotted line represents a situation of stress with reduced reproductive investment: Prolactin levels increase faster during the laying phase, reaching therefore quicker the upper threshold that triggers the end of the laying phase (black dotted arrow). This faster rate of prolactin increase is therefore associated with a reduced clutch size. B. A schematic representation of changes in prolactin levels in response to stress during the molting phase. The black solid line represents a situation without stressor: Prolactin levels decrease after the breeding phase and the molt starts (black solid arrow) when prolactin levels reach a lower threshold (gray dotted line). The rate of this decrease determines therefore the onset of molt (see also Dawson (2006)). The black dotted line represents a situation of stress: Prolactin levels decrease slower, and reach therefore later the lower threshold that triggers the onset of molt (black dotted arrow). This slower rate of prolactin decrease is therefore associated with a delayed molt.

determination (Fig. 4A). Therefore, the prolactin stress response may be a hormonal mechanism that aims to reduce the clutch size when environmental conditions are not appropriate for reproduction. This is particularly interesting if pre-breeding individuals are able to modulate their prolactin response to stress as suggested by the study from Opel and Proudman (1986) because the prolactin response to stress could then be directly linked to reproductive effort in laying birds.

The potential of prolactin as a link between environmental stress and egg laying or/and clutch size has been overlooked in wild birds. However, this hypothesis is somewhat supported by findings issued from studies on poultry. Rozenboim et al. (2004) found that heat stress was associated with a simultaneous increase in prolactin levels, a decrease in LH and steroid secretion and a dramatic reduction of egg production in pre-breeding domestic turkeys. Maney et al. (1999b) also found that temperature can affect prolactin secretion in pre-breeding white-crowned sparrows (*Zonotrichia leucophrys*). Moreover, other studies have reported that vasoactive-intestinal peptide immunization leads to reduced prolactin levels and increased egg laying production, suggesting therefore a major effect of prolactin secretion in the termination of egg laying, and therefore, in the control of clutch size (El Halawani et al., 1995, 2000). An experimental increase in prolactin levels also results in a decreased egg production in turkeys (Youngren et al., 1991). However, the relationship between stress, prolactin and egg production remains unclear because egg production could be reduced in a context of stress even if prolactin levels are maintained experimentally low (Rozenboim et al., 2004; Mobarkey et al., 2013). Some studies also failed to find any correlation between prolactin levels and LH levels (e.g. Small et al., 2007; Schaper et al., 2012; Ryan et al., 2014) suggesting that prolactin and LH levels or egg production may be uncoupled under some circumstances (such as in determinate layers that always lay the same clutch size). Because of this potential disconnection between prolactin levels and egg laying, other specific hormones could be involved and play a major role in clutch size determination (Rozenboim et al., 2004; Mobarkey et al., 2013). Serotonin is known to inhibit the reproductive endocrine axis (El Halawani et al., 1983), and to be closely linked to prolactin levels or its precursors (Hargis and Burke, 1984; El Halawani et al., 1988). In that context, future studies should further disentangle the relationships that link stress, prolactin and serotonin in pre-breeding birds in order to better understand the role of prolactin as a potential mediator of the impact of environmental stressors on clutch size determination.

Prolactin, stress and re-nesting decision

Because of its potential role in both the initiation of breeding and the termination of the parental phase (Silver, 1984; Hall et al., 1986; Sharp et al., 1998; Sockman et al., 2006), prolactin could logically be involved in re-nesting behavior in multiple brood species. In addition to photorefractoriness, the maintenance of moderately elevated prolactin levels after the first breeding event could inhibit re-nesting and relaying because of its anti-steroidogenic effects (El Halawani et al., 1991; Dawson and Sharp, 1998, but see Wingfield et al. (1989)). Supporting this hypothesis, prolactin levels decrease between breeding events in several multiple brood species (Goldsmith et al., 1981; Goldsmith, 1982; Silverin, 1991), whereas they remain elevated after the parental phase in some single brood species that may show relative refractoriness only (e.g. Garcia et al., 1996; Lormée et al., 1999). Moreover, Jouventin and Mauget (1996) triggered re-laying by experimentally reducing prolactin levels in failed breeders of king penguins, demonstrating therefore the role of this hormone in the regulation of re-nesting behavior. This suggests that, in addition to photoperiod, prolactin could orchestrate the reproductive cycle of birds by inhibiting or facilitating re-nesting at the end of previous annual breeding event. However, this statement is not always supported since prolactin levels remain elevated between breeding events in some multiple brood species (Hiatt et al., 1987; Wingfield & Goldsmith 1990). Because of these discrepancies, it remains unclear to what extent prolactin and the prolactin response to stress could functionally influence the decision to re-nest in multiple brood species. When individuals are not breeding, prolactin levels usually increase in response to stress (see the Stage-dependent prolactin stress response section; Riou et al., 2010; Angelier et al., 2013). By maintaining prolactin levels above a threshold, stressors or poor environmental conditions may therefore inhibit re-nesting and re-laying because of the anti-steroidogenic effects of prolactin (El Halawani et al., 1991; Dawson and Sharp, 1998). Therefore, the prolactin stress response might play a role by inhibiting relaying in multiple brood species. It may also mediate the decision to relay or not in the species that can lay a replacement clutch. To better understand the role of prolactin in mediating re-nesting decision, future studies should experimentally test these hypotheses and also examine the relationship between re-nesting decision, environmental stressors, and prolactin levels in other single brood and multiple brood species.

Prolactin, stress and the onset of molt

There is also strong evidence that the beginning of the post-breeding molt is governed by changes in prolactin levels (Kuenzel, 2003; Dawson, 2006). Prolactin levels drop at the end of the parental phase when parental activities decrease or even stop and the post-breeding molt life-history stage starts a few days after (Crossin et al., 2012). For instance, Deviche et al. (2000) showed that both the post-breeding decrease in prolactin levels and the onset of molt occur earlier in young Dark-eyed juncos relative to older juncos and Dawson et al. (2009) found that both the decrease in prolactin levels and the onset of molt were delayed in males relative to females in mute swans. Dawson and

Sharp (1998) also experimentally showed that molt does not occur if the seasonal photoperiod-related cycle of prolactin levels is suppressed in European starlings. All these findings strongly suggest that a pre-breeding surge in prolactin secretion followed by the post-nuptial decrease in prolactin levels may be required to trigger the onset of molt (i.e. transition from the breeding phase to the molt stage, Dawson and Sharp, 1998; Dawson, 2006; Fig. 4B).

In response to stress, prolactin levels of some species seem to increase in failed breeders but also in breeders towards the end of the parental phase (Riou et al., 2010; Angelier et al., 2013). Therefore, environmental stressors could delay the onset of molt in birds by maintaining elevated prolactin levels, and thus, by delaying the post-breeding decrease in prolactin levels (Fig. 4B). Although this hypothesis has to our knowledge never been tested, a recent study supports this idea. It showed that environmental conditions could simultaneously affect prolactin levels and the initiation of molt in castrated starlings: reduced temperature led to the maintenance of elevated prolactin levels for a longer period and this maintenance was associated with a delayed onset of molt (Dawson and Sharp, 2010). Future experimental studies should test this hypothesis by assessing the influence of environmental stressors and/or prolactin levels on the onset of molt in birds.

Conclusions and perspectives

Does prolactin orchestrate reproductive-related life-history decisions?

In this paper, we have summarized our current knowledge regarding the functional link between parental behavior and prolactin in birds. Despite a clear connection between prolactin and the parental phase, we have demonstrated the complexity of this link. We have also shown that prolactin levels are affected by environmental, energetic and stressful conditions in parent birds and we have additionally highlighted that prolactin regulation could be disrupted by contaminants with ultimate consequences on parent birds. Finally, we have emphasized that prolactin levels could predict breeding success under some circumstances. At the proximate level, this functional link between environmental conditions, prolactin, parental behavior and breeding success suggests that prolactin is involved in the regulation of parental decisions in birds. Interestingly, we have also highlighted that the prolactin and the corticosterone stress responses seem complementary because they may interact to mediate the physiological and behavioral responses of parent birds to environmental constraints. We believe that future experimental studies should investigate how these two hormones interact. These studies should also focus on the regulation of prolactin (the response of prolactin levels to vasoactive intestinal peptide and dopamine) and on the receptors (location, density, and changes through time) that mediate the action of this hormone on behavior and physiology. Field studies would certainly benefit from focusing on both the corticosterone and the prolactin stress response when investigating the hormonal regulation of parental investment. Finally, we have reviewed current evidence about the potential role of the prolactin stress response in mediating other life-history decisions, such as the timing of molt and the determination of clutch size. This has led to new hypotheses regarding the potential of prolactin to orchestrate the annual life history cycle of birds.

Modulation of the prolactin stress response?

At the ultimate level, the ability of individuals, populations and species to modulate their prolactin stress response may be crucial to investigate if prolactin is involved in so many life-history decisions (clutch determination, parental effort, and timing of molt). The prolactin response to stress may be a mechanism allowing parents to adjust their behavior to their current environmental situation in order to optimize their fitness. In that respect, the modulation of the corticosterone stress response has been intensively used to investigate parental decisions. To our knowledge, only a few studies have however focused on the modulation of the prolactin stress response (reviewed in Angelier et al. (2013); Wojczulanis-Jakubas et al. (2013); Angelier et al. (2015)) despite its potential link with all these decisions (Dawson, 2006; Sockman et al., 2006; Angelier and Chastel, 2009).

Environmental constraints and stressors can affect prolactin levels and this prolactin stress response seems to avoid individuals to invest resources into specific activities (laying, parental behavior, re-nesting, or molting) if they will not provide any fitness benefits (e.g. large clutch or high parental effort under poor environmental conditions). Under some ecological circumstances, investing resources into these specific activities could, however and counter-intuitively be beneficial to fitness (e.g. the terminal investment theory). In that context, a potential prolactin resistance to stress could therefore be crucial because they could allow individuals to engage into specific activities or behaviors despite poor environmental conditions. Here we have summarized a few ecological situations where individuals should theoretically down-regulate their prolactin response to stress (Table 2). Future studies should test these hypotheses to understand to what extent the prolactin stress response can be helpful when investigation life-history decisions.

Table 2
Potential role of the prolactin stress response during the laying, the parental, and the molting phase and evolutionary logic behind a prolactin resistance to stress during these three phases. Under circumstances, we hypothesize that individuals should down-regulate their prolactin stress response in order to maintain their laying, parental and molting effort, and thus, to optimize their fitness.

Life-history stage	Potential role of prolactin	Action of the prolactin stress response	Logic for a prolactin resistance to stress	Examples
Laying phase	Clutch size determination	Reduced clutch size	When the value of the current reproduction is elevated	Low nest predation risk, cues of good environmental conditions, mate of high quality
			When the parent has a low residual reproductive value	Old individuals,single annual brood species, infected individual
			When the costs of producing eggs are low	Good food situation, low adult predation risk, mild temperature
Parental phase	Parental effort	Reduced parental effort	When the value of the current reproduction is elevated	Large brood of high quality, low nest predation risk, mate of high quality
			When the parent has low residual reproductive value	Old individuals, single annual brood species, infected individual
			When most of parental care depends on one parent	In monoparental care reproductive mode
			When the cost of parental care are low	Good food situation, low adult predation risk, mild temperature
Molt phase	Timing of molt	Delaying the onset molt	When the molting window is short	Migrant birds, birds living at high latitudes
			When the energetic conditions are optimal	High food availability, mild temperature
			When the costs of reduced locomotor activity are low	Low predation risk, low territoriality

To conclude, the prolactin stress response has been overlooked and needs to be further investigated because it has a strong potential to allow ecological physiologists to better understand how individuals adjust their life-history decisions (clutch size, parental behavior, renesting, and onset of molt) according to the environmental conditions they encounter. We hope that this review and these perspectives will elicit further research on that topic.

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