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

Frédéric Angelier [a,*], John C. Wingfield [b], Sabrina Tartu [a], Olivier Chastel [a]

[a] Centre d'Etudes Biologiques de Chizé, CNRS, UMR 7372, 79360 Villiers en Bois, France
[b] Department of Neurobiology, Physiology and Behavior, University of California, One Shields Avenue, Davis, CA 95616, USA

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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.

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

* Corresponding author.
E-mail address: angelier@cebc.cnrs.fr (F. Angelier).

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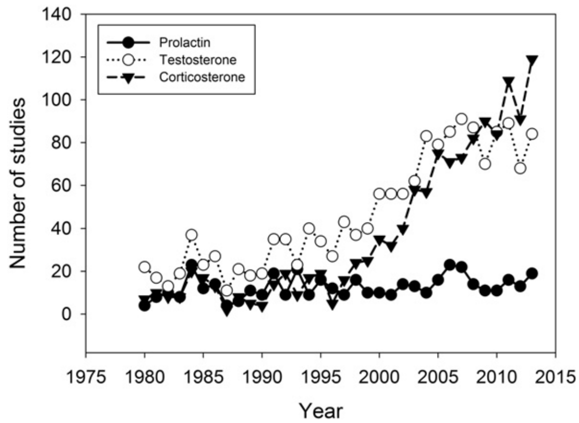

Fig. 1. Trends in the number of studies published each year on different hormones from 1980 to 2013. These numbers were found by conducting a search in ISI Web of Knowledge (search terms: corticosterone, testosterone, prolactin and bird, search date: January 15 2015).

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-

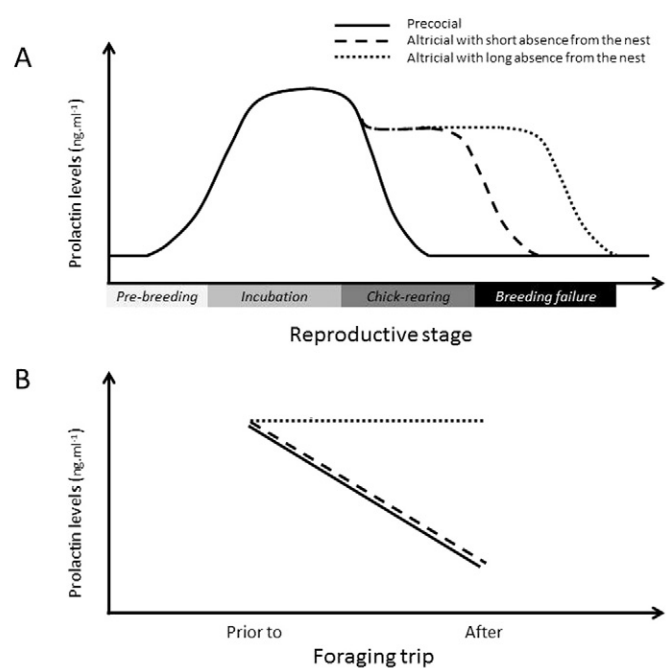

Fig. 2. A. A schematic representation of the prolactin cycle of breeding birds with different reproductive modes (precocial such as fowls, ducks and geese; altricial with short absence from the nest such as gannets, starlings, and doves; altricial with long absence from the nest such as penguins, albatrosses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