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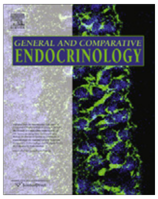

Changes in plasma hormone levels correlate with fledging in nestling Leach's storm-petrels

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ABSTRACT

Leach's storm-petrels accumulate large amounts of body mass throughout the nestling period. Approximately 4 days before fledging, nestlings weigh 50–100% more than adults. In order to shed this excess mass, nestlings engage in behavioral anorexia, and leave the burrow when they are light enough to fly. During this prefledging period, we measured several plasma hormones (corticosterone, thyroxine, and testosterone) to determine whether the behavioral changes associated with fledging are correlated with endocrine changes. In several species, including petrels, corticosterone levels are known to increase near fledging. Reduced food consumption has been shown to elevate corticosterone levels and decrease thyroxine levels in nestling birds. In nestling storm-petrels, levels of both corticosterone and thyroxine increased. Storm-petrels were found to secrete measurable levels of testosterone, but levels did not change during the prefledging period. Increased corticosterone levels might be part of an endocrine signal that initiates changes in feeding behavior, or may result from reduced food intake. Elevated thyroxine levels may be related to metabolic changes involved in mass loss. Future experimental work is needed to ascertain whether the described endocrine changes are responsible for, or result from, prefledging changes in petrel feeding behavior.

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1. Introduction

At fledging, nestling birds begin the transition from complete dependency on their parents to being self-sufficient. Both endogenous and exogenous factors are associated with fledging. In multi-nestling broods, competition for limited food or space within the nest may induce nestlings to leave (Lemel, 1989; Nilsson, 1990). For seabirds, the metabolic and/or endocrinal changes that result from altered feeding behavior are thought to mediate fledging (Vinuela and Bustamante, 1992; Gjerdrum, 2004). For example, in some species of pelagic seabirds, parents feed their nestlings less near the time of fledging (Gray and Hammer, 2001). In other species, fledging is preceded by a period of anorexia, regardless of food availability (Mauck and Ricklefs, 2005).

Corticosterone is thought to be an important mediator of fledging. Birds respond to environmental, physiological, and social challenges with activation of the hypothalamic–pituitary–adrenal (HPA) axis, leading to increased corticosterone secretion (Silverin, 1998; Cockrem, 2007). Elevated corticosterone allows birds to adjust to challenges by enhancing lipogenesis and protein catabolism (Gray et al., 1990; Silverin, 1998), and by increasing available glucose (Kettlehut et al., 1988; Jenni et al., 2000). Increased corticosterone can promote foraging in adult birds (Lohmus et al., 2006) and begging in nestlings (Kitaysky et al., 2001a). Chronically elevated corticosterone can, however, depress growth and functioning of the immune, reproductive, and nervous systems (Sockman and Schwabl, 2001; Kitaysky et al., 2003).

Baseline levels of corticosterone increase near fledging in a number of altricial and semi-altricial species, including pied flycatchers (*Ficedula hypoleuca*) (Kern et al., 2001), northern mockingbirds (*Mimus polyglottos*) (Sims and Holberton, 2000), canaries (*Serinus canaria*) (Schwabl, 1999), American kestrels (*Falco sparverius*) (Heath, 1997; Love et al., 2003), thin-billed prions (*Pachyptila belcheri*) (Quillfeldt et al., 2007a) and white storks (*Ciconia ciconia*) (Corbel and Groscolas, 2008). In snowy owls (*Bubo scandiacus*) (Romero et al., 2006), however, no change is observed. Increased corticosterone levels might be related to stress associated with impending fledging (Heath, 1997), or reduced food intake (Corbel and Groscolas, 2008), and this increase has been correlated with increased locomotion (Belthoff and Duffy, 1998; Breuner et al., 1998; Corbel and Groscolas, 2008). Elevated corticosterone during

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the prefledging period might benefit young birds by promoting flight and foraging skills.

Levels of thyroid hormones (T_3 and T_4) also appear to change near fledging for species that undergo prefledging fasting and molting (Corbel et al., 2008). Thyroid hormones are required for growth and maturation of muscles, and trigger cartilage differentiation and ossification in skeletal tissues. An important regulator of molting and feather synthesis (Groscolas and Cherel, 1992), thyroid hormones also control metabolic and thermogenic processes (Silva, 1995; McNabb and Olson, 1996). In nestling king penguins (*Aptenodytes patagonicus*), thyroid hormones decline during winter fasting and then increase during the spring molt. These increased levels of thyroid hormones are correlated with increased locomotor activity. Hormone levels, particularly thyroxine (T_4), then begin to decline and reach baseline at fledging. In king penguins, T_4 might be involved in signaling molt status. High levels of T_4 may indicate that molt is ongoing and inhibit fledging. After feather growth is complete, time to fledging is directly related to circulating T_4 (Corbel et al., 2008).

The hormonal control of fledging has been investigated in only a few species, most of which are altricial. Altricial species develop rapidly, are regularly fed by their parents, and are usually reared in multi-nestling broods. Petrels (procellariiformes) are semi-altricial, and exhibit different life-history characteristics that include slow development and little to no parental care. Leach's storm-petrels (*Oceanodroma leucorhoa*) nest in underground burrows and lay a single egg (Huntington et al., 1996). Both males and females share incubation, which lasts 40–44 days (Huntington et al., 1996). Once hatched, the storm-petrel nestling is brooded for 5 days, and then remains unattended for 55–65 days before fledging. Nestlings often weigh between 1.5 and 2 times adult mass near the end of the nestling period. The excess mass of storm-petrel nestlings consists mostly of fat (Ricklefs et al., 1980), and has been regarded as insurance against stochastic variation in food provisioning (Obst and Nagy, 1993; Ricklefs and Schew, 1994; Hamer and Hill, 1997). Before nestlings are capable of sustained flight, this excess fat must be lost. Flight-feather growth is complete at approximately 60 days of age, and this point has been termed *T* by Mauck and Ricklefs (2005). *T* is characterized by a number of behavioral and physiological changes that prepare the nestling for fledging. Although parents continue to bring food to their nestlings, prefledging storm-petrels engage in behavioral anorexia and consequently lose mass. The body temperature of nestlings increases during this period (Weathers et al., 2000), and nestlings accumulate stomach oils (Obst and Nagy, 1993). Approximately 4 days later, the nestlings leave the burrow.

In this study, we examine the degree to which hormonal changes are associated with the behavioral and physiological changes that characterize fledging in Leach's storm-petrels. In particular, we investigated whether hormonal changes might initiate or result from the behavioral anorexia that precedes fledging. Anorexia has been documented in adult birds during incubation (Sherry et al., 1980) and molting (Cherel et al., 1988), as well as in both procellariiform seabird nestlings (Philips and Hamer, 1999) and penguin nestlings (Cherel and Le Maho, 1985). The endocrine system is believed to initiate re-feeding in fasting adult penguins (Robin et al., 1998). In particular, increased baseline levels of corticosterone are believed to contribute to re-feeding behavior after prolonged fasting (Robin et al., 1998). Whether hormonal changes contribute to anorexia in adult or nestling birds has not been investigated.

Concentrations of corticosterone, T_4, and testosterone were repeatedly measured in nestlings during the 10 days preceding fledging. We speculated that if hormonal changes are caused by reduced food intake, then differences should be observed after *T* is reached and birds begin to fast. Because reduced food intake has been shown to elevate corticosterone levels in nestling birds (Kitaysky et al., 2001b), we suspected that corticosterone might increase after fasting is initiated. Limited food intake is also associated with decreasing levels of thyroid hormones in several avian species (Sharp and Klandorf, 1985; Le Ninan et al., 1988). Therefore, we anticipated that T_4 levels might be highest before fasting was initiated, and then gradually decrease as fledging neared. Alternatively, if corticosterone or T_4 were involved in initiating changes in petrel feeding behavior, we expected that levels should change before or near the onset of fasting. While not directly implicated in fledging, testosterone is known to influence many aspects of physiology and behavior in birds, including metabolic rate (Hannsler and Prinzinger, 1979; Feuerbacher and Prinzinger, 1981), lipid storage (Wingfield, 1984), and timing of molt (Runfeldt and Wingfield, 1985). Because baseline levels of testosterone in seabirds have not been well studied, we also characterized testosterone levels in nestling petrels and determined whether these levels change during the prefledging period.

2. Methods

2.1. Study population and sample collection

This study was conducted from August through September in 2003 and 2004 at the Bowdoin Scientific Station on Kent Island in the Bay of Fundy, New Brunswick, Canada (44°35′N, 66°45′W). The study population was a breeding sub-colony of approximately 500 actively nesting Leach's storm-petrel pairs, from which different subsets of burrows were sampled in 2003 ($n = 19$) and 2004 ($n = 25$). Only two burrows were used in both years of the study. Given the high nest-site fidelity on Kent Island (Huntington et al., 1996), this insured that all but two nestlings were the product of different pairs of parents.

During 2003 and 2004, nests were checked daily to determine the day of hatching. From approximately 54 days of age until 65 days of age, nestling growth was monitored at 2-day intervals. Nestlings were removed from their burrows by hand. Wing length was measured to the nearest mm, and nestling mass to the nearest 0.1 g with a portable electronic balance (OHAUS Inc.) at approximately the same time each day. Fledging was assumed when nestlings were no longer within the burrow.

Blood samples were collected within 1–2 min of initial handling. For each sample, heparinized microcapillary tubes were used to collect 150–200 μL of whole blood from the brachial vein, alternating wings at each sampling interval. Samples were kept cool for less than 3 h before centrifugation and plasma removal. Between 50 and 100 μL of plasma was frozen at −20 °C for storage and transport, then at −80°C until analysis. In total, 215 plasma samples were analyzed, and 219 mass and wing-length measurements were collected from 44 nestlings. All procedures were carried out in accordance with the guidelines set by the Institutional Animal Care and Use Committee of Kenyon College.

2.2. Plasma hormone analysis

Because of their limited volume, plasma samples were transferred to 2 ml Eppendorf tubes and diluted 1:2 with phospho-buffered saline (PBS). Samples were mixed with a vortex, and a volume of 100% ethanol equal to the PBS/plasma mixture was added to precipitate proteins and lipids, giving a dilution factor of 1/4 for each sample. Upon adding ethanol, the samples were again mixed using a vortex, and allowed to incubate at room temperate for 10 min. Samples were then spun at 12,282*g* in a centrifuge for 10 min to remove the lipid fraction. The supernatant was

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