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Energetic constraints and parental care: Is corticosterone indicative of energetic costs of incubation in a precocial bird?

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ABSTRACT

Suppression of the adrenocortical response (e.g., corticosterone release) to an acute stressor is a physiological adjustment thought to decrease the likelihood of avian parents abandoning their nests. However, some periods of parental care, like incubation, are energetically costly, thus corticosterone could increase during these stages to allow incubating parents to utilize energy reserves. Wood ducks (*Aix sponsa*) have ~30 day incubation periods and only the female incubates the eggs. We hypothesized that corticosterone would be important in regulating energy availability during incubation in this species. Because resources invested in reproduction increase with clutch size, we also hypothesized that clutch size would influence plasma corticosterone during incubation. We measured baseline and stress-induced corticosterone in incubating females during early and late stages of incubation. At both stages of incubation all hens had low baseline corticosterone levels. However, we found that stress-induced corticosterone was 105% greater late in incubation than early in incubation. We also detected a significant negative correlation between female body mass and stress-induced corticosterone late in incubation, but not during the early stages of incubation. Furthermore, we found a significant positive relationship between stress-induced corticosterone and clutch size. These lines of evidence support the hypothesis that incubation in wood ducks is energetically costly and corticosterone is important in supporting the energetic demands of incubating hens. Our findings suggest that corticosterone's role in supporting parental care behaviors are dynamic and are influenced by several factors and that there is a greater physiological cost associated with incubating larger clutches.

Introduction

Birds exhibit tremendous parental care, investing substantial time and resources to rear their young. For many birds the investments that parents make during incubation can have implications for both their current and future reproductive success (Hanssen et al., 2005; Heaney and Monaghan, 1996; Reid et al., 2000a). During incubation birds can have 20–50% higher metabolic rates than non-incubating birds (reviewed in Tinbergen and Williams, 2002), and experimentally increasing clutch size or experimentally altering nest temperatures can affect the size of subsequent clutches, parental survival and immune responses, chick fledging success, and can increase parental metabolic rates during incubation (de Heij et al., 2006; Hanssen et al., 2005; Reid et al., 2000a,b; Tinbergen and Williams, 2002). The energetic cost of incubation can be particularly steep for uniparental incubators that receive no aid from their mate. For instance, female common eiders (*Somateria mollissima*) rarely feed during their ~26 day incubation period and receive no assistance from males. During this time, females lose up to 23–46% of their body mass (Bolduc and Guillemette 2003; Parker and Holm 1990).

Parents navigate the conflicting demands of activities necessary for successful reproduction and those required to maintain their own body condition and survival via a suite of orchestrated physiological signals, including hormones (Ricklefs and Wikelski, 2002; Wingfield and Sapolsky, 2003). Hormonal changes that occur during reproduction include alterations in an individual's physiological response to acute stress, most notably the effects of acute stress on corticosterone and prolactin concentrations. Under most circumstances, corticosterone increases and prolactin decreases in response to acute stress in birds (Angelier and Chastel, 2009). Corticosterone is an important hormone in energy regulation and during times of acute stress it shunts resources towards survival, whereas prolactin is a hormone important in promoting parental care behaviors (Angelier and Chastel, 2009; Buntin, 1996; Vleck, 1998). Increases in corticosterone can inhibit parental care behaviors by redirecting resources towards activities necessary for survival and by negatively affecting plasma prolactin concentrations (Angelier et al., 2009; Silverin,

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1986). Thus, according to the parental care hypothesis (Holberton and Wingfield, 2003; O'Reilly and Wingfield, 2001; Wingfield et al., 1995) many birds should maximize their current reproductive success despite potential risks to survival by dampening their physiological response to acute stressors when caring for young in an effort to reduce the likelihood of abandoning their offspring. Such a strategy is particularly relevant if an individual is not likely to have future opportunities to reproduce and thus investing in their current brood has higher value than future reproductive potential (Jessop, 2001; Wingfield and Sapolsky, 2003). The parental care hypothesis supports the idea that seasonal variation in corticosterone results from corticosterone's role in modulating behavior (Romero 2002). Indeed, many birds attenuate hormonal responses to stress during times of parental care, and the degree to which physiological responses to acute stress change can vary among and within species, with factors such as parental age, breeding stage, breeding experience, clutch size, and length of the breeding season influencing the magnitude and persistence of hormonal changes (Angelier et al., 2006; Angelier and Chastel, 2009; Bokony et al., 2009; Goutte et al., 2010; Heidinger et al., 2006; Lendvai et al., 2007; Romero et al., 1997; Schmid et al., 2011; Silverin and Wingfield, 1998). For instance, in breeding pairs of three species of shorebirds the parent exhibiting more parental care had lower stress responses than the parent exhibiting less parental care, whereas both sexes in a fourth species with equivalent biparental care had similar stress responses. (O'Reilly and Wingfield, 2001). Additional data suggest that dampening of corticosterone responses to stress should also vary with the “value” of the brood (the brood value hypothesis), whereby larger broods have higher reproductive value resulting in greater reductions in corticosterone responses to stress (Lendvai et al., 2007).

Although many studies demonstrate that adrenocortical responses to stress decrease during periods of intense parental care and support the parental care hypothesis, caring for young is energetically expensive (Tinbergen and Williams, 2002; Williams, 1996) and glucocorticoids, like corticosterone, are important for maintaining energy balance. Many birds lose considerable weight during the most demanding periods of parental care, and increases in corticosterone could be important in fueling parental behaviors by catabolizing energy stores. Indeed, the energy mobilization hypothesis (Romero, 2002) was one of several hypotheses developed to help explain seasonal variation in baseline and stress-induced corticosterone, whereby animals upregulate corticosterone release during times of high energy demand. For most birds, the highest plasma concentrations of baseline and stress-induced corticosterone correspond with the breeding season (Romero, 2002). Presumably, the relative energy demands of different parental care behaviors vary across the altricial-precocial spectrum, and circulating levels of glucocorticoids should be highest during the most energetically costly parental care stage. For example, in altricial tree swallows (*Tachycineta bicolor*), Bonier et al. (2009) detected a significant negative relationship between clutch size and corticosterone levels in female tree swallows during incubation, but a positive relationship between baseline corticosterone levels of the parent and brood size during chick-rearing, the most demanding parental care stage for this species. In precocial birds, the most demanding period of parental care is incubation, and weight loss can be substantial during this period (e.g., Parker and Holm 1990; Prince et al., 1981) suggesting that elevated glucocorticoids might be important for mobilizing energy stores during incubation. Indeed, a study in magellanic penguins which fast during incubation detected a significant increase in baseline and stress-induced corticosterone in incubating parents from early to late in incubation (Hood et al., 1998; also see Kitaysky, et al., 1999 for a similar finding in kittiwakes). In addition, stress-induced corticosterone late in incubation negatively correlated with body mass in incubating penguins, further suggesting the possible importance of corticosterone in liberating energy stores in precocial birds as they lose mass during incubation.

One additional factor that could influence the energetic demands of incubation is clutch size because incubating larger clutches requires more energy than smaller clutches (Tinbergen and Williams, 2002; Williams, 1996). Furthermore, experimental manipulation of clutch size can result in greater mortality and lower immune responses, brood success, and future reproductive effort of incubating parents (de Heij et al., 2006; Hanssen et al., 2005; Larsen et al., 2003; Reid et al., 2000b), clearly demonstrating that caring for larger broods comes with costs. Contrary to the brood value hypothesis which predicts a negative correlation between stress-induced corticosterone and clutch size (Lendvai et al., 2007), energy constraints can elevate both baseline and stress-induced corticosterone (McEwen and Wingfield, 2003; Romero et al., 2009; Sapolsky et al., 2000) suggesting that parental corticosterone levels could scale positively with clutch size during incubation, particularly in precocial species with uniparental incubation. This effect should be further exaggerated in species that experience brood parasitism because clutch sizes can become particularly enlarged.

In this study we investigated changes in adrenocortical responses to stress from early to late incubation in female wood ducks (*Aix sponsa,* Linneaus), a waterfowl species with highly precocial young that has an average incubation period of 30 days (range: 27–37 days; Hepp and Bellrose, 1995). This species exhibits uniparental incubation in which only the female incubates the eggs and receives no aid from males during this time (Hepp and Bellrose, 1995). Wood ducks exhibit high incubation constancy (>80%), but they take approximately two breaks a day to forage (Folk and Hepp, 2003; Manlove and Hepp, 2000). Although the energetic deficit female wood ducks experience during incubation is probably not as substantial as it can be for species that undergo fasting during incubation (e.g., Eiders and some penguins), females do tend to lose ~5% of their body mass during the incubation period (Hepp et al., 1990). This decrease in body mass supports the idea that incubation is energetically demanding for wood duck hens and elevated concentrations of corticosterone may be necessary for mediating incubation in this species. To test the energy mobilization hypothesis we measured baseline and stress-induced corticosterone concentrations of incubating female wood ducks at both an early stage of incubation (d3–8) and at a late stage of incubation (d22–28). Specifically, we predicted that 1) corticosterone would increase with incubation period because incubation is energetically costly, and the cumulative energetic deficit should increase with time spent incubating, 2) corticosterone would increase with clutch size because larger clutches require more energy to incubate than smaller clutches, and 3) corticosterone would be highest late in the nesting season because younger females and females of lower body weight nest later in the season than heavier, more experienced females (Hepp and Kennamer, 1993).

Materials and methods

Study species

The wood duck (*Aix sponsa*) is a widely distributed dabbling duck whose breeding range extends throughout much of the eastern half of North America and along the west coast from southern California to British Columbia (Hepp and Bellrose, 1995). Wood ducks are relatively small-bodied (~650–700 g) and occupy a diversity of aquatic habitats, including freshwater marshes, wooded swamps, beaver ponds, and bottomland habitats along major tributaries (Bellrose and Holm, 1994). Female wood ducks nest in tree cavities, but will also use artificial nest boxes, a characteristic that facilitates locating nests and capturing females (Hepp et al., 1987). In our study area in the southeastern U.S., wood ducks initiate nesting in mid-late February and continue nesting until mid-July. Females can produce multiple broods in a breeding season.

Although wood ducks are socially monogamous and begin to form pair bonds in autumn and winter (Ambruster, 1982; Hepp and Bellrose, 1995), only the female cares for the eggs and ducklings (Fredrickson, 1990). Females lay one egg per day and the average clutch