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Optimizing the trade-off between offspring number and quality in unpredictable environments: Testing the role of differential androgen transfer to collared flycatcher eggs

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ABSTRACT

According to the brood reduction hypothesis, parents adjust their brood size in response to current environmental conditions. When resources are abundant, parents can successfully raise all hatched offspring, but when resources are scarce, brood reduction, i.e., the sacrifice of some siblings to secure the quality of a subset of offspring, may maximize fitness. Differential transfer of maternal androgens is one potential proximate mechanism through which female birds may facilitate brood reduction because it may alter the relative competitive ability of sibling nestlings. We tested the hypothesis that female collared flycatchers (*Ficedula albicollis*) manipulate sibling competition by transferring less androgens to eggs late in the laying sequence. We experimentally elevated androgen levels in i) whole clutches and ii) only the two last laid eggs, and compared growth and begging behavior of offspring from these treatments with a control treatment. By using three treatments and video assessment of begging, we examined the effects of within-clutch patterns of yolk androgen transfer on levels of sibling competition in situ. When androgens were elevated in only the two last laid eggs, begging was more even among siblings compared to control nests. We also found that female nestlings receiving additional yolk androgens showed higher mass gain later in the breeding season, while their male counterparts did not. Our results suggest that females may improve reproductive success in unpredictable environments by altering within-clutch patterns of yolk androgen transfer. We discuss the possibility that life-history divergence between the co-occurring collared and pied flycatcher (*Ficedula hypoleuca*) is amplified by patterns of yolk androgen transfer.

Introduction

In species with extensive parental care, such as many bird species, parents must resolve a trade-off between offspring number and the ability to provide sufficient resources to ensure offspring success and a high probability of recruitment into the breeding population (Lack, 1947). One way for parents to optimize the number of offspring that recruit into the breeding population is by producing more offspring than they can raise under normal resource conditions (Husby, 1986; Lack, 1947). If resources are abundant, parents can in this way raise more offspring than under normal conditions. However, when resources are scarce, some of the offspring may starve; the parents should choose to provide resources to a subset of their offspring in order to raise some high quality offspring, and not merely many poor quality offspring. This strategy, in which parents adjust their brood size to current resource conditions, is known as the brood reduction hypothesis (e.g., Husby, 1986; Lack, 1947).

Mothers may optimize the trade-off between offspring number and quality in unpredictable environments by mediating levels of sibling competition (Marshall et al., 2008). If offspring are approximately equal in competitive ability, resources should be distributed evenly among siblings. If resources are scarce, however, equality in sibling competitive ability may not be optimal for parental fitness because none of the offspring may be of high enough quality to successfully recruit into the breeding population (Husby, 1986). By placing some offspring at a competitive disadvantage, and thereby reducing sibling competition among the other offspring, mothers may facilitate brood reduction.

One proximate mechanism by which female birds may mediate relative sibling competitive ability in the nest is through altering the

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level of androgen hormones, such as testosterone and androstenedione, experienced by their developing offspring (reviewed in Gil, 2008; Groothuis et al., 2005a). Testosterone in the yolk has been found to affect or correlate with a variety of offspring phenotypes, including growth, begging intensity, immune function, and survival (e.g., Groothuis et al., 2005b; Müller et al., 2010; Pilz et al., 2004; Schwabl, 1996; Sockman and Schwabl, 2000; von Engelhardt et al., 2006). Maternal transfer of androgens can vary both among females (Pilz et al., 2004; Tobler et al., 2007; Tschirren et al., 2009) and among eggs within a single clutch (Gil et al., 2006; Hegyi et al., 2010; Schmaltz et al., 2008; Schwabl, 1993; Sockman and Schwabl, 2000). The latter pattern, i.e. within-clutch variation in yolk androgens, may be an adaptive mechanism by which females can influence relative sibling competitive ability (reviewed in Gil, 2008; Groothuis et al., 2005a). Two general patterns of within-clutch variation in yolk androgens have been observed: an increase in yolk androgen levels over the laying sequence, and a decrease over the laying sequence. For species showing an increase over the laying sequence (e.g., pied flycatchers, Gil et al., 2006; red-winged blackbirds, Lipar et al., 1999; smooth-billed anis, Schmaltz et al., 2008; canaries, Schwabl, 1993; American kestrels, Sockman and Schwabl, 2000), enhanced amounts of androgens in later-laid eggs may offset any competitive disadvantage caused by hatching asynchrony (Lipar et al., 1999; Schwabl, 1993; but see Sockman and Schwabl, 2000) and lead to greater similarity in sibling competitive ability. By contrast, for species showing decreasing yolk androgen levels over the laying sequence (e.g., American coots, Reed and Vleck, 2001; cattle egrets, Schwabl et al., 1997), females may increase the competitive disparity among siblings, which may facilitate brood reduction when resources are scarce (Schwabl et al., 1997).

In this study, we tested whether differential transfer of maternally derived androgens to the eggs of collared flycatchers (*Ficedula albicollis*) may explain observed seasonal patterns of offspring survival. The survival probability of collared flycatcher nestlings declines over the breeding season (Qvarnström et al., 2009), as does food availability (Veen et al., 2010). Because parental strategies should adjust to offspring growth strategies (and vice versa; reviewed in Müller et al., 2007a; Tobler and Smith, 2010), we predicted that female collared flycatchers should respond to their offspring's poor ability to cope with unpredictable resource levels late in the breeding season. There are at least two possible ways by which female collared flycatchers could do this. First, they could lay a smaller clutch later in the season to reduce sibling competition for food. Second, they could manipulate the competitive ability of nestlings within the clutch. The steep decline in both clutch size and nestling survival as the breeding season progresses (Qvarnström et al., 2009) suggests that females have adopted a mixture of the two strategies. Thus, they appear to partly adjust their clutch size to the decline in predictability of resources, but not fully (a perfect adjustment would result in no increased mortality rate). Because the increased mortality rate over the breeding season is consistent with brood reduction, we hypothesized that female collared flycatchers may influence competitive disparity among siblings by transferring a lower amount of androgens to the last laid eggs in the clutch. To test this hypothesis, we used a manipulative field experiment in which we altered the yolk androgen content of natural clutches and subsequently measured morphological and behavioral responses in offspring raised in natural nests.

Methods

The collared flycatcher, *F. albicollis*, is a small, insectivorous passerine. It winters in southeastern Africa and migrates to summer breeding grounds in central and Eastern Europe and the Swedish islands of Öland and Gotland. This study was conducted during May–June 2008 on collared flycatchers breeding in nestboxes on the Baltic island of Öland, Sweden (57°10′ N, 16°58′ E). The breeding season begins in late April, when male flycatchers begin to arrive and compete over breeding territories (Pärt and Qvarnström, 1997; Qvarnström, 1997). Females arrive approximately one week later, and after inspecting a number of males and their territories, select their mates and commence nest building. The breeding areas consist of deciduous and mixed coniferous–deciduous forest plots stretching across much of the island (see Qvarnström et al., 2009 and Figures 1 and 3 therein for more details on forest plot locations). Females lay one egg per day, with an average clutch size of about 6 eggs (Alatalo et al., 1990). After a 12-day incubation period, the eggs hatch, whereupon both parents feed insects to the nestlings. At 14–15 days post-hatching, the nestlings reach adult weight, and fledge from the nest. Fledglings in good condition, with relatively higher body mass for a given body size, have increased chances of recruitment into the breeding population (Lundberg and Alatalo, 1992).

To test our hypothesis that female collared flycatchers can affect levels of competitive disparity among siblings through within-clutch variation in androgen transfer, we manipulated egg androgen content in each clutch using three different injection treatments (described in greater detail below): 1) a control treatment, 2) a complete clutch androgen treatment in which all eggs in the clutch received additional androgens, and 3) a two last-laid eggs androgen treatment in which only the last two eggs laid in the clutch received additional androgens. We predicted that these androgen treatments would affect the level of competitive disparity in the nest by altering the begging intensity of those nestlings receiving additional androgens. A more intensely begging nestling should be more likely to beg first and receive food from a parent. Thus, if females transfer less androgens to last-laid eggs, and nestlings hatched from these eggs beg less intensely than their siblings, they may be less competitive than their siblings and receive less food. We therefore predicted that the intensity of the begging behavior of nestlings within clutches receiving the two last-laid eggs androgen treatment should be less variable than within nests receiving the other two treatments. We also predicted lower variance in nestling mass within clutches receiving the two last-laid eggs androgen treatment. Finally, if maternal androgen transfer influences begging intensity, we predicted that the complete clutch androgen treatment should lead to an overall increase in feeding rate compared to the control treatment. Most studies of the effects of yolk androgen transfer on offspring traits include only a control and a whole-clutch androgen treatment (e.g., Barnett et al., 2011; Müller et al., 2008; Pitala et al., 2009; von Engelhardt et al., 2006). By adding a third treatment (the two last-laid eggs treatment), we were able to investigate both the effects of yolk androgen transfer in general, and the effects of within-clutch patterns of yolk androgen transfer on levels of sibling competitive disparity.

All experimental procedures adhered to the standards established by the United States National Institutes of Health and were approved by the local Swedish Ethical Committee on Animal Research (Drn 27-08) and the Bird Ringing Centre of the Swedish Museum of Natural History (Stockholm, Sweden; License number 605).

Egg handling

We began monitoring the nestbox plots for new collared flycatcher nests in late April. Upon location of a nest with three eggs or fewer, we marked each egg with a non-toxic marking pen. We then returned to the nest every day and marked each new egg with its order in the laying sequence. On the day it was laid, we collected the fourth-laid egg from every nest for a different experiment and replaced it with a dummy egg made from modeling clay. We continued daily visits to each nest, marking each new egg, until no new eggs were laid and incubation had started. On the fourth day of incubation, we collected the entire clutch of eggs and replaced them all with dummy eggs.