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Blood metabolite levels in normal and handicapped pied flycatchers rearing broods of different sizes

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Abstract

We measured levels of select metabolites (glucose, triglycerides, free fatty acids, glycerol, uric acid) and corticosterone in the blood plasma of adult pied flycatchers *Ficedula hypoleuca* while they were rearing broods whose sizes were modified experimentally. We also made it more difficult than normal for some pairs of birds to forage by removing certain wing and tail feathers (handicapping them). Both procedures have been shown previously to change parental workload. We did this in order to determine if the birds alter their use of nutrients in response to differences in their workload. Metabolite levels were not influenced by handicapping or brood size. However, the concentration of free fatty acids in the plasma of females and of triglycerides in the plasma of males was directly related to the frequency with which the adults fed their nestlings. These findings suggest that the two sexes have different ways of coping with the work associated with rearing the brood: females apparently undergo brief daily fasts while feeding their chicks, whereas males take more time to feed themselves while providing food for their young, and spend more time doing so as their workload increases. The flycatchers exhibited high concentrations of uric acid and corticosterone in the blood plasma; corticosterone and glycerol were positively correlated in females; and corticosterone and triglyceride levels were negatively correlated in males; all of which suggest that gluconeogenesis provides some of the energy required for their parental activities.

Keywords: Plasma metabolites; Corticosterone; *Ficedula hypoleuca*; Parental behavior; Pied flycatcher

1. Introduction

Parental investment theory (Clutton-Brock, 1991; Daan and Tinbergen, 1997) predicts that the effort parent birds devote to rearing a brood will depend in part on the likelihood that their nestlings will survive to be recruited into the breeding population. If parents feed their chicks at high rates, the nestlings will likely grow rapidly and leave the nest at a large size. This in turn will improve their chances of survival, and hence the potential lifetime reproductive success of their parents. Indeed, the survival of nestlings has been shown on many occasions to depend on their mass or size at fledging (Martin, 1987; Lindén et al., 1992). Pied flycatchers *Ficedula hypoleuca*, for example, do not usually survive their first year unless their tarsi are longer than 18.5 mm and they weigh more than 13 g when they fledge (Lundberg and Alatalo, 1992). We would therefore predict that any increase in brood size or difficulty in procuring food for the chicks would be accompanied by a corresponding increase in parental investment in the brood, i.e., in the energy the adults expend while rearing their chicks, unless the additional cost is so high that it reduces the adults' future fecundity (Gustafsson and Sutherland, 1988) or postbreeding survival (Askenmo, 1979), or makes them more susceptible to disease (Gustafsson et al., 1994).

Several studies show that the number of times that parent flycatchers visit the nest to feed the nestlings per hour varies directly with the size or age of the brood (Von Haartman, 1954; Silverin, 1981; Lifjeld and Slagsvold, 1988; Källander and Smith, 1990; Török and Toth, 1990; Lundberg and Alatalo, 1992). The 17–20 h (800 or more deliveries of food) that the parents spend providing their chicks with food each day must

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represent a considerable energetic drain on them, which is probably why flycatchers, particularly females, commonly lose weight while rearing their broods, often in amounts that depend on brood size (Winkel and Winkel, 1976; Askenmo, 1977; Källander and Smith, 1990; Török and Toth, 1990). This daily energy expenditure (DEE), 46–91 kJ/day, has been measured by Moreno et al. (1995, 1997) and is about four times the birds' basal metabolic rate.

Such sizeable increases in the expenditure of energy on the part of the adults ought to be accompanied by changes in their use of nutrients and therefore measurable by variations in the metabolite levels of their blood. For example, we might expect to find that the birds mobilize glycogen, fat, and perhaps even protein from body stores. This would, in turn, reduce their plasma glucose (as passerines store very small amounts of glycogen, less than enough to provide the energy for 1 h at normal rates of energy consumption [Swain, 1991]) and triglyceride levels and simultaneously elevate plasma levels of free fatty acids, glycerol, and uric acid (Brackenbury and El-Sayed, 1984; Swain, 1987, 1992; Jenni-Eiermann and Jenni, 1996, 1997; Hõrak et al., 1999). The degree of mobilization of fat and protein, in particular, would presumably depend on how much effort the adults were expending and on their nutritional state (fat reserves) when the nestling phase begins.

If, however, the adults do *not* normally work at highly taxing rates while rearing their chicks unless environmental conditions are extremely adverse, or if their weight loss at this time is an energy-saving adaptation that improves their foraging efficiency and thereby reduces the costs associated with feeding the brood, as proposed by Freed (1981) and Norberg (1981), then variations in their blood metabolites would presumably be independent of factors like brood size or provisioning rates. Many studies of passerines, among them pied flycatchers, have already shown that levels of key plasma metabolites respond quickly to fasting and activities associated with the rearing of broods of chicks (Swain, 1987, 1992; Jenni and Jenni-Eiermann, 1996; Jenni-Eiermann and Jenni, 1991, 1996, 1997; Hõrak et al., 1999). Our study was designed to extend such studies by examining how differences in brood size and the foraging ability of adult pied flycatchers affect levels of these metabolites and corticosterone (as an indicator of gluconeogenesis) in their blood.

2. Materials and methods

2.1. Study sites and ambient conditions

Our study involved pairs of pied flycatchers (*F. hypoleuca*) breeding in nest boxes at four study sites within oak and mixed deciduous woods near Newbridge-on-Wye, Wales (52°13′N, 3°27′W) during May and June, 1998 and 1999. Average minimum (7.9 and 8.8 °C) and maximum (17.0 and 17.2 °C) ambient temperatures were similar during the time when chicks were developing in both years of the study, but 1998 was wetter (rainfall = 13.4 cm in 42 rain days vs. 6.1 cm in 47 rain days during 1999). Furthermore, there was no obvious peak in the abundance of caterpillars (which the birds feed their chicks) during the nestling period in 1999.

2.2. Experimental design

During the nestling period in both years, we modified brood size and handicapped half of the pairs to alter their workload. We subsequently collected blood samples from the parents during the period when their chicks are growing at a maximum, linear rate in order to measure metabolite and corticosterone levels in the plasma. We also recorded parental feeding visits to the nest during this phase of nestling development. When the adults were captured, we immediately took a sample of their blood and then weighed them using a Pesola balance (±0.1 g); measured the length of the tarsus using calipers (±0.05 mm) and the length of the wing chord and second primary remigial feather using a plastic ruler (±0.5 mm); and then ringed them. We also weighed and measured some (1999) or all (1998) of the chicks in each brood at 3-day intervals as they grew. These measurements included the mass and the length of the tarsus, wing chord, and second primary remigial feather (counting inward from the distal margin of the wing).

2.2.1. Changes in brood size

We only used flycatchers whose clutch size was 7 to preclude any possible differences in parental behavior that might be related to differences in the fecundity of a female. We swapped young birds between nests within 3 days after they hatched in order to create broods of five, seven, and nine chicks. (The average brood size at our study sites is 7 chicks.) For purposes of control, two chicks were exchanged between nests when the number of chicks was the same as the number that hatched. It is common for one or two chicks to die during the nestling period, however, and in the end our broods consisted of 4–5, 6–7, and 8–9 chicks.

2.2.2. Handicapping the adults

In addition, we handicapped both parents in half of the broods using the procedure of Lifjeld and Slagsvold (1988; also see Slagsvold and Lifjeld, 1988) in which primaries 7 and 9 (counting inward from the distal margin of the wing) from both wings and the six central rectrices are removed. In this case, the feathers were cut off at the base with scissors. This was done during incubation (females) or the first 3 days of the nestling period (males and some females). The clipped feathers did not regrow (i.e., were not replaced) during the experiment. Such handicapping has been shown previously to increase the "cost of foraging", by making it more difficult for pied flycatchers to capture food, and to reduce the rate at which females feed their chicks by about 30% (Lifjeld and Slagsvold, 1988; Slagsvold and Lifjeld, 1988). However, handicapped adults do not abandon their broods.

2.2.3. Monitoring parental behavior

We observed the number of visits of the adults to their broods during one, 30-min period sometime between 07:30 and 18:00 h on day 5 or 6 of the brood period (day 0 = the day on which the