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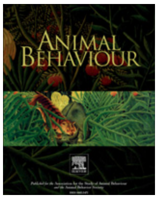

Sex-biased parental investment is correlated with mate ornamentation in eastern bluebirds

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Males typically have greater variance in reproductive success than females, so mothers should benefit by producing sons under favourable conditions. Being paired with a better-than-average mate is one such favourable circumstance. High-quality fathers can improve conditions for their offspring by providing good genes, good resources, or both, so females paired to such males should invest preferentially in sons. Ornamentation has been linked to male quality in many birds, and, in support of differential allocation theory, females of several avian species invest more in entire broods when paired to attractive mates. Additionally, the females of some bird species apparently manipulate the primary sex ratio of their broods in relation to the attractiveness of their mates. However, empirical support for a link between mate ornamentation and preferential feeding of sons (another form of biased investment) is lacking. We tested for correlations between sex-biased parental investment and mate plumage colour in the eastern bluebird, *Sialia sialis*, a species in which juveniles have sexually dichromatic UV blue plumage. We found that the proportion of maternal feeding attempts to fledgling sons (versus fledgling daughters) was positively correlated with structurally coloured plumage ornamentation of fathers. Additionally, paternal feeding attempts to sons were correlated with plumage ornamentation of mothers and increased in fathers that had breast plumage characteristics typical of older males. These results provide further support for the idea that parental strategies are influenced by mate attractiveness and provide the first evidence that mate ornamentation can influence parental behaviour even after offspring have left the nest.

When the benefits of producing male and female offspring vary depending on context, parents are expected to maximize reproductive success by investing differentially in sons and daughters depending on their circumstances (Trivers & Willard 1973; Charnov 1982). Differential investment in sons and daughters can occur by varying the ratio of sons and daughters produced, or through differential investment of energy in sons and daughters after birth or hatching. Animals have been shown to adjust investment in sons versus daughters in relation to season (Dijkstra et al. 1990; Sakisaka et al. 2000; Schultz 2008), diet (Bradbury & Blakey 1998; Opit & Throne 2008), maternal age (Blank & Nolan 1983; Isaac et al. 2005), mate quality (Svensson & Nilsson 1996; Roed et al. 2007) and mate attractiveness (Sheldon et al. 1999). In birds, differential investment in sons and daughters can take the form of primary sex-ratio manipulation via changes in the proportion of male eggs in a given brood. Alternatively, sex-biased investment strategies can manifest as differential resource allocation, which may occur if parents invest time and effort differently in sons and daughters after hatching.

The disparity in the value of males versus females stems from different reproductive opportunities for males and females of different qualities. In many species of animals, males have greater variance in reproductive output than females because the investment in offspring by females is larger than the investment by males (Bateman 1948; Clutton-Brock 1988). Greater variance in male reproductive success arises because poor-quality males are likely to produce fewer offspring than are poor-quality females, whereas high-quality males can produce more offspring than can high-quality females. Therefore, parental investment in sons should be higher if (1) mothers are in good condition (Trivers & Willard 1973), or (2) if sons are fathered by high-quality males (Charnov 1982). Because high-quality males can provide a suite of direct (e.g. increased levels of food provisioning and nest defence; Hoelzer 1989) and indirect (e.g. heritable genetic quality) benefits to their

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offspring (Andersson 1994), and because these benefits increase the likelihood that superior offspring will be produced, relative levels of parental investment in sons should also be influenced by the quality of their father.

Total parental investment in birds, typically measured in terms of investment to an entire brood, has been shown to vary with mate ornamentation in several species including blue tits, *Cyanistes caeruleus* (Limbourg et al. 2004), barn swallows, *Hirundo rustica* (de Lope & Møller 1993), and zebra finches, *Taeniopygia guttata* (Burley 1988). Female blue tits, for example, feed broods at higher rates when mated to males with bright UV coloration (Limbourg et al. 2004) and defend their nests more vigorously than do females paired to males with dull UV plumage (Johnsen et al. 2005). In contrast to these examples, female eastern bluebirds, *Sialia sialis*, do not feed nestlings at higher rates when mated to highly ornamented males (Siefferman & Hill 2003). Although no evidence has yet been published that supports the relationship between mate attractiveness and sex-biased provisioning for any avian species, bluebird parents may assess the ornamentation of their mates when making feeding decisions within a brood, altering relative investment in sons versus daughters.

We examined the potential for sex-biased parental investment via differential provisioning to sons and daughters in the eastern bluebird, a strongly sexually dichromatic species with sexually dichromatic offspring (Gowaty & Plissner 1998; Siefferman & Hill 2008). Because conspicuous sexual dichromatism is rare in juvenile birds (Kilner 2006) and presents a clear mechanism by which parents can distinguish sons from daughters, bluebirds present an ideal system in which to study sex-biased provisioning (sensu Stamps 1990). Additionally, extrapair paternity is high in some populations of eastern bluebirds (Gowaty & Plissner 1998), potentially providing the reproductive variance between males and females required by the Trivers & Willard (1973) investment theory.

The bright UV blue structural plumage coloration of adult male eastern bluebirds is positively correlated with male provisioning rates to incubating females (Siefferman & Hill 2005a), male provisioning rates to nestlings (Siefferman & Hill 2003), body condition and age (Siefferman et al. 2005). Melanin-based, orange-coloured, breast plumage of males also varies with age, with older males possessing brighter breast feathers with less-red chroma (Siefferman et al. 2005). Because males with more colourful structural plumage feed incubating females and nestlings at higher rates and are generally older and more experienced, we predicted that females would adjust their resource allocation to sons and daughters according to the ornamentation (perceived quality) of their mates. Specifically, females mated to colourful males should increase their investment in sons because having a bright male as a mate should increase the quality of those sons. Because the structural plumage of adult female eastern bluebirds is a condition-dependent trait that varies with food intake and predicts reproductive success in the wild (Siefferman & Hill 2005b), males also stand to benefit by modifying allocation to sons and daughters relative to the coloration of their mates. Thus, we also predicted that adult male bluebirds should increase their investment in sons when mated to more colourful females.

To test these predictions we examined the provisioning rate of bluebird parents to fledgling sons and daughters. When offspring were of fledging age, we placed one daughter and one son in a divided cage and allowed the parents to forage freely. Parents quickly adapted to the trial set-up and provisioned offspring through the wire cage. We analysed feeding rates of parents as a proportion of feeding attempts to sons versus daughters and examined the relationship between this proportion and the plumage ornamentation of each individual's mate.

MATERIALS AND METHODS

Study Population

We studied a banded population of eastern bluebirds (hereafter, bluebirds) in Lee County, Alabama, U.S.A. (32°35′N, 82°28′W) between March and August 2008. Bluebirds are a sexually dimorphic passerine species (family Turdidae) that breeds throughout eastern North America (Gowaty & Plissner 1998). Adult male bluebirds have rich blue coloration on their heads, backs, rumps, tails and wings. The upper breasts of adult males are orange, and the bellies are white. Adult females have blue–grey upper parts with dull blue wings and tails and pale orange breasts.

We monitored nestboxes throughout the breeding season to determine when nests were in use by bluebirds, as well as to monitor the age and development of bluebird offspring. Bluebirds typically begin laying during the month of March in central Alabama and can produce up to three broods, averaging approximately four eggs per clutch ($\bar{x} \pm \mathrm{SE} = 3.75 \pm 1.1$; Siefferman & Hill 2007), over the course of the breeding season. Nestlings typically hatch after 14 days of incubation and fledge 15–20 days after that (Gowaty & Plissner 1998).

Trial Procedures

Because fledglings spend much of their time hidden, it is typically difficult to observe patterns of parent–offspring interactions after young have fledged. In our study, we constrained the movements of fledgling bluebirds to an observation arena while simultaneously allowing their parents to forage naturally. Between 16 and 18 days of age, we selected one male and one female nestling from nests that contained one male nestling and at least one female nestling. We determined the sex of fledglings using plumage characteristics in the field, but later performed molecular techniques that allowed us to double-check our field assignments. Eastern bluebird nestlings typically fledge near this stage of development (Gowaty & Plissner 1998), and we chose specific trial dates on a brood-by-brood basis depending on the development and size of nestlings in each nestbox. When broods contained multiple female nestlings, we selected the individual with the mass closest to that of the male nestling.

On the day of the trial, we gathered all nestlings from each box to measure their mass. To minimize the effects that different hunger levels might have on fledgling begging rate and intensity, as well as the effects that such differences might have on parental provisioning patterns, we fed each nestling one mealworm (*Tenebrio molitor*) before all members of the brood were returned to the natal nestbox. At this point, we sealed the entrance to the nestbox to prevent any feeding by parents, as well as any premature fledging attempts. We then left the immediate area for 30 min to allow the nestlings to digest the recently consumed mealworm. After the 30 min pretrial period, we returned to the nestbox, selected the predetermined male and female, and placed them separately in a divided wire cage near the natal nestbox (Fig. 1). A solid partition prevented physical and visual contact between siblings in the wire cage. To create a location from which bluebird parents could assess their offspring, we placed a 50 cm tall perch 1 m away from the front of the cage. We kept all remaining nestlings in a cloth box and fed them mealworms throughout the duration of the trial.

Parent bluebirds quickly adjusted to the trial set-up and began to feed their offspring through the wire mesh of the cage. We used a tripod mounted video camera (Sony Hi-8) to record parent and chick interactions for 1 h, at which point we reversed the position of the fledglings in the cage (to control for possible effects of cage location) and resumed recording for one additional hour. After each trial, we removed the fledglings from the cage and returned them to their nestbox along with their siblings.