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Evidence that fathers, but not mothers, respond to mate and offspring coloration by favouring high-quality offspring

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Parents have limited resources and, when simultaneously rearing multiple offspring, are expected to favour particularly valuable offspring. Because offspring characteristics like sex and ornamentation influence future reproductive value, these traits may influence parental favouritism. Parents in high-quality nest environments should prefer sons because sons show greater variability in reproductive potential than daughters. Moreover, when ornamental plumage coloration is condition dependent, parents should favour brighter over duller sons. We tested parental favouritism for fledgling-aged eastern bluebirds, *Sialia sialis*, a species in which fledglings display condition-dependent UV-blue coloration on their wings and tails. We simultaneously threatened two offspring with mock predators and recorded which offspring the parents defended. In accordance with the predicted value of offspring, fathers protected brighter over duller sons and protected sons over daughters when mated to high-quality mates. Mothers did not discriminate between sons and daughters or between brighter and duller sons. These results suggest that ornamental plumage coloration in juvenile bluebirds functions as a signal in father–offspring interactions. Paternal and maternal responses of eastern bluebirds to offspring characteristics may differ because of differences in parental allocation strategies or because males assess offspring quality based on variation in plumage coloration, a trait that also functions in competitive interactions among adult males.

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Among passerine birds, predation is one of the most important factors affecting nestling survival (Ricklefs 1969); however, behaviours associated with defending offspring are often risky and can result in injury, or even death, of the parents. Once fledglings leave the nest, parents face trade-offs in time and energy when rearing multiple offspring and thus should act to maximize their fitness by preferentially protecting offspring with the best direct fitness prospects (Trivers 1972). If they are to protect their offspring based on the future reproductive value of these individuals, parents should benefit from being able to accurately assess the condition of their offspring (Clutton-Brock 1991).

Parent–offspring conflict is expected because parents should benefit from discriminating between high- and low-quality offspring while all offspring should attempt to signal vigorously for limited parental resources (Trivers 1974). For example, offspring often signal to parents by begging; nestlings that beg more frequently or more intensely often preferentially receive their parents' attention (e.g. Price & Ydenburg 1995; Leonard & Horn 1996). Indeed, begging behaviours are often reliable signals of need but not necessarily of nestling quality (Kilner & Johnstone 1997), whereas nestling size (e.g. Price & Ydenburg 1995; Shiao et al. 2009) and plumage coloration (e.g. Krebs & Putland 2004; Avilés et al. 2011) can indicate quality.

Among adult birds, plumage coloration is often an honest and reliable indicator of individual quality that signals information to potential mates and competitors (reviewed in Hill & McGraw 2006). Plumage coloration could also function as an honest signal of offspring quality to parents. Because nestlings rarely display ornamental plumage, however, the signalling function of nestling plumage coloration has been studied in only a few species. Experimentally manipulated natal environments reveal that structurally based plumage coloration is a condition-dependent trait in both nestling blue tits, *Cyanistes caeruleus* (Johnsen et al. 2003; Jacot & Kempenaers 2007) and eastern bluebirds, *Sialia sialis* (Siefferman & Hill 2007). Thus, in these species, parents could use variation in plumage coloration to discriminate between high- and low-quality offspring. Indeed, offspring plumage coloration has been shown to influence parental favouritism. American coot, *Fulica americana*, parents preferentially feed nestlings with unaltered ornamental

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plumes over nestlings that have had their plumes dulled (Lyon et al. 1994). Subsequently, multiple studies have demonstrated that nestling plumage influences provisioning decisions (Galvan et al. 2008; Tanner & Richner 2008; Griggio et al. 2009; Ligon & Hill 2010a). To date, only one study has tested how nestling plumage coloration influences favouritism as measured by parental defence behaviours (Griggio et al. 2009). Predicting how offspring sex influences parental favouritism is more complex. Because males have greater variance in reproductive potential than females, differences in individual quality have greater impacts on male than on female reproductive success (Trivers & Willard 1973). Thus, high-quality sons should be more valuable than high-quality daughters. Likewise, average-quality or low-quality daughters should be more valuable than average-quality or low-quality sons. Additionally, parents may perceive the reproductive event as higher quality when paired with a high-quality mate and this may change reproductive investment (Burley 1977). Therefore, if parents perceive a reproductive bout as high quality, they may favour sons over daughters (Trivers & Willard 1973). Despite this, few studies test parental favouritism towards sons versus daughters (Mock & Forbes 1995) and most of those have been equivocal (Teather 1992; Leonard et al. 1994; Michler et al. 2010; but see Mainwaring et al. 2011). More commonly, researchers have demonstrated that mothers manipulate the sex ratio of broods in response to their perception of the nest environment. For example, when paired with highly ornamented mates, female blue tits produce male-biased broods (Sheldon et al. 1999; Delhey et al. 2007).

Mothers and fathers, however, may not be equally likely to discriminate among offspring or may be expected to bias favouritism towards different offspring (Lessels 2002). In species that exhibit biparental care of offspring, females typically invest more heavily in producing eggs and incubating young while males typically invest more energy in defending the territory or nest from competitors and predators (Wesolowski 1994). Males could potentially benefit more than females by discriminating between offspring based on quality because their overall reproductive investment is lower or because their confidence in paternity is lower than the females' confidence in maternity (Lessels 2002).

We investigated whether eastern bluebird parents show favouritism when defending their fledgling-aged offspring from potential predators. Our study had three primary goals. We designed experiments such that parents could only defend one of two offspring at a time, and parents were given (1) offspring of different sexes and (2) male offspring that differed in plumage coloration. Because male fledglings in better body condition are significantly brighter than those in poorer condition (Siefferman & Hill 2007), we predicted that parents should favour brighter sons. We expected that favouritism for sons versus daughters should be influenced by the parents' perception of their mate's quality. We predicted that individuals mated to more ornamented (higher-quality) mates would favour sons over daughters. Our third goal was to test whether parents differed in favouritism behaviour. Because males provide most of the care to fledgling-aged young but invest less in overall parental care (Gowaty & Plissner 1998), we predicted that males may be more likely to discriminate among fledglings.

METHODS

Study Species

Eastern bluebirds are socially monogamous passerines that readily breed in nestboxes (Gowaty & Plissner 1998). In the mountains of North Carolina, U.S.A., their reproductive season lasts from early May to early August, and parents can produce one or two successful broods (~4 nestlings per brood) per season. Nestlings hatch synchronously, and both males and females provision offspring and defend the nest (Pinkowski 1978). Bluebirds show a range of behaviours when defending their young, from retreating from potential nest predators to diving at and attacking the threat (Gowaty & Plissner 1998). Females allocate greater energy to egg laying and incubation (Pinkowski 1977), while males devote more time and energy to postfledgling care (Gowaty & Plissner 1998).

Eastern bluebirds show sexually dichromatic UV-blue structural plumage coloration as both adults and juveniles. Among adults, plumage coloration is correlated with mate quality: brighter, more UV-chromatic males and females feed offspring more often and achieve higher reproductive success (Siefferman & Hill 2003, 2005a). Male coloration also likely signals resource-holding potential: brighter males are more likely to obtain high-quality nest sites (Siefferman & Hill 2005b). By the age of 13 days posthatch, juveniles display blue coloration on their wings and tails. First-year bluebirds undergo only a partial moult during their first autumn, thus second-year birds display the wing and tail coloration that they acquired as nestlings (Gowaty & Plissner 1998). Because fledglings are dichromatic, parents should be able to recognize the sex of offspring. Moreover, in this species, the blue coloration is condition dependent in both adults and nestlings (Siefferman & Hill 2005a, 2007), suggesting that parents can predict nestling condition by assessing plumage coloration.

Study Sites, Nest Monitoring, Measurements and Identification

From April to August 2010, we studied a population of breeding eastern bluebirds in rural Watauga County, NC (36°17′59″N, 81°40′33″W) where we monitored 180 nestboxes. Once the offspring started to hatch (first nestling hatches = day 1), each nestling was uniquely identified with coloured markers (Sharpie™ marker). We returned to the nests every 3 days to measure nestling body mass and the length of tarsi and wings on days 2, 5, 8, 11 and 14 posthatching. When the nestlings were 8 days old, we fitted them with a numbered aluminium U.S. Fish and Wildlife Service band. Once the nestlings reached fledging age (approximately 15–18 days posthatch), we collected 2 cm of feathers from the distal end of the left and right fifth primary of each nestling for spectrophotometric analysis. Additionally, we captured and banded the parents of each brood and collected eight feathers from the rump of each adult for spectrophotometric analysis.

Field Experiment

Our goal was to simulate conditions that parents experience just after their offspring have fledged from the nest; thus, we conducted the experiment just prior to natural fledging (within days of fledging). We commenced the first trial when offspring were near fledging age (between age 14 and 18 days), when primary wing feathers had emerged >2 cm from the feather sheath. At this stage, fledglings can only fly short distances (<2 m), move primarily by hopping, cannot forage on their own, and are still under the care of their parents (Gowaty & Plissner 1998).

For each pair of breeding bluebirds, we conducted two experiments of parental favouritism on 2 consecutive days. On the first day, the trial tested parental preferences for male versus female offspring. On the second day, the trial tested parental preferences for duller versus brighter male offspring. For each trial, we placed two nestlings in separate wire cages (71 × 46 × 11.5 cm) at opposite ends of a 5 m transect, equally distant from the nestbox. Adjacent to each cage, we erected a 50 cm perch for the parents. Above each cage, we hung a replica of an American crow, *Corvus brachyrhynchos* (This Place is a Zoo, Snohomish, WA, U.S.A.) as a 'threat' to the

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