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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.

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

offspring to invoke parental defence behaviour. We played an audio recording of crow calls and cries of eastern bluebird nestlings. We placed a video camera 10 m from each set-up to record parental behaviour. Additionally, we watched each trial from a distance of 40 m, using binoculars and a voice recorder. We quantified the behaviour of each parent separately (Fig. 1). Following each trial, we returned all the nestlings to their nests.

For the first trial ($N = 34$), we chose two offspring of opposite sex but of similar size, and randomly assigned them to a cage. In the second trial ($N = 22$), we chose two males and randomly assigned one male to the dulled treatment and one male to the brightened treatment. Wing feathers were dulled using a black Sharpie™ marker and brightened using a violet mist Prismacolor™ marker. In some trials (opposite sex: $N = 4$; same sex: $N = 6$), we did not have appropriate nestlings; thus, we moved two nestlings from another nest of similar age (±1 day). However, more than one pair of parents never chose between the same dyad of siblings. During both experiments, the nestlings were chosen such that they were most similar in mass, tarsus length and wing length to reduce the likelihood that other morphological characteristics would influence parental favouritism.

Using both digital videos and voice recordings, one researcher (N.L.B.) quantified the behaviour of the male and female parents separately. Each parent was given a numerical score of the most intense behaviour it showed in defence of each nestling, such that more aggressive behaviours were scored higher than less aggressive ones: (1) absent, (2) present but ignoring trial, (3) watching silent, (4) chattering, (5) diving one to two times, (6) diving three to five times, (7) physically striking the predator, (8) diving more than five times, (9) physically striking the predator more than once. Any trial in which the parent's score for both nestlings was the same was excluded. We also determined the percentage of time that each parent spent on the side of each nestling by calculating the number of seconds spent with each nestling divided by the total number of seconds spent with any nestling multiplied by 100. If a parent spent more than 55% of the time near one offspring, we scored that nestling as the favourite. Any trial for which a nestling did not receive more than 55% of the parental attention was excluded.

Plumage Coloration Analysis

One researcher (N.L.B.) measured plumage coloration of the wing feathers of each male nestling used in the trials and the rump coloration of all parents using an Ocean Optics S2000™ spectrometer (range 250–880 nm; Dunedin, FL, U.S.A.) with a micron fibre-optic probe to record spectral data at a 90° angle to the feather surface. From these spectral curves, we determined brightness, UV chroma and hue. Mean brightness was calculated as the average of the total reflectance from 300 to 700 nm. UV colour was calculated as the average of the proportion of the total reflectance that was within the UV range ($\int$ 300–400 nm/$\int$ 300–700 nm). Hue was calculated as the wavelength with the highest reflectance. We only quantified brightness and UV chroma for nestlings because the reflectance curves were relatively flat, making hue measures inaccurate. The wing feathers of the male offspring were collected prior to the colour manipulation in the field. Thus, we measured both the original plumage coloration and manipulated plumage coloration.

Statistical Analysis

All data were collected on parents' first broods of the season. We used Wilcoxon signed-ranks tests to verify that nestlings that had been experimentally manipulated differed in plumage coloration (brightness and UV chroma). We used chi-square or Mann–Whitney *U* tests to determine whether parents (1) more aggressively defended one sex of offspring over the other, (2) more aggressively defended brighter or duller male offspring, (3) spent more time with male versus female offspring and (4) preferred brighter versus duller sons. However, because parental preferences were qualitatively the same when we used time and level of aggressiveness to ascertain the chosen offspring, we only report favouritism based on time in all future analyses. Because we expected that the nest environment would influence parental preferences for offspring sex, we used backward stepwise logistic regressions to determine whether mate coloration (brightness, UV chroma and hue) influenced parental favouritism. Finally, we used Pearson correlations to test whether the strength of parental preferences was correlated with differences in offspring coloration. In all analyses, we tested favouritism of mother and fathers separately and then used chi-square tests to determine whether mothers and fathers made similar choices. Sample sizes vary because some trials ended in a tie, some parents did not respond to the experiment and we failed to measure plumage coloration for some adults.

Ethical Note

We minimized the time that fledglings were out of the nestbox, and all nestlings were returned to their nests within 1 h of the start of each trial. Observations of fledglings post-trial suggest that the protocol did not reduce fledgling survival. The trials were conducted on sequential days, and in only one case did nestlings fledge before the onset of the second trial (we ran fewer male–male trials because there were fewer nests with two male nestlings than there

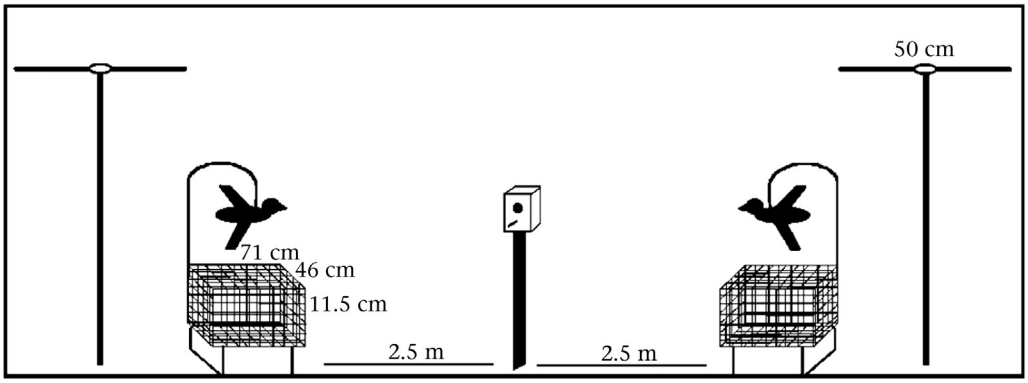

Figure 1. Nestling bluebirds were placed separately in two wire cages; each cage had a replica of an American crow hanging above it. One cage was placed at each end of a transect with the nestbox located in the centre. Adjacent to each cage, we placed 50 cm perches for parents. We used the same experimental set-up when parents chose between offspring of different sex and between experimentally brighten and dulled male offspring.

were nests with at least one male and one female nestling). This study was approved by the Appalachian State University Animal Care and Use Committee (IACUC project number 08-4) and conducted under North Carolina State and U.S. Fish and Wildlife Service permits.

RESULTS

Parental Favouritism for Male versus Female Offspring

We conducted 34 trials of offspring sex, but one of the parents did not respond aggressively in seven trials (mother: $N = 3$; father: $N = 4$). Moreover, nine trials ended in a tie. Mothers and fathers were significantly more likely to favour one offspring than to show no favouritism (mothers: $\chi^2_{1,31} = 5.45$, $P = 0.02$; fathers: $\chi^2_{1,30} = 4.80$, $P = 0.03$). A backward stepwise logistic regression revealed that the parents' likelihood of showing favouritism or lack of favouritism (a tie) towards offspring sex was not influenced by their mates' coloration (best model: mothers: $\chi^2_{1,25} = 4.39$, $R^2 = 0.16$, $P = 0.22$; fathers: $\chi^2_{1,31} = 0.54$, $R^2 = 0.02$, $P = 0.91$).

Backward stepwise logistic regression revealed that a mother's preference for offspring sex was not influenced by her mate's coloration (best model: $\chi^2_{1,16} = 0.45$, $R^2 < 0.01$, $P = 0.50$). Fathers, however, were more likely to favour male offspring when their mates were highly ornamented (i.e. greater UV chroma and hues shifted towards lower wavelengths; model: $\chi^2_{1,18} = 7.26$, $R^2 = 0.32$, $P = 0.03$; mate rump brightness: $\beta = -29.24$, Wald = 1.11; mate rump hue: $\beta = 0.16$, Wald = 3.69; Fig. 2a, b).

When we disregarded mate ornamentation, there was no evidence that mothers or fathers expressed favouritism for sons or daughters. Mothers spent the majority of their time defending male offspring in 50% of the trials (chi-square test: $\chi^2_{1,22} < 0.01$, $P = 1.00$). Fathers spent the majority of their time defending male offspring in 62% of the trials ($\chi^2_{1,21} = 1.19$, $P = 0.28$).

Parental Favouritism for Brighter versus Duller Males

After manipulation, experimentally brightened sons were significantly brighter than their experimentally dulled brothers (Wilcoxn signed-ranks test: $Z = -4.11$, $N = 22$, $P < 0.01$; Fig. 3); thus, the manipulation succeeded in altering offspring plumage coloration. Nestling UV chroma, however, did not differ significantly between experimentally brightened and dulled sons after manipulation ($Z = -1.19$, $N = 22$, $P = 0.24$).

We conducted 22 trials using brightened versus dulled sons, but one of the parents did not respond aggressively in six trials (mother: $N = 3$; father: $N = 3$). Eight trials ended in a tie ($N = 3$ mother trials, $N = 5$ father trials). Parents were significantly more likely to show favouritism for one offspring than to show no favouritism (mothers: $\chi^2_{1,19} = 8.90$, $P = 0.003$; fathers: $\chi^2_{1,19} = 4.26$, $P = 0.04$).

Mothers showed no favouritism for brighter or duller male offspring; they preferentially defended brightened offspring in 56% of the trials ($\chi^2_{1,16} = 0.25$, $P = 0.62$). Fathers showed a significant preference to defend the brightened offspring; fathers defended brighter sons in 79% of trials ($\chi^2_{1,14} = 4.57$, $P = 0.03$; Fig. 4). The strength of parents' favouritism was not influenced by differences in plumage brightness of experimentally brighter and duller male offspring (Pearson correlation: mothers: $r_{20} = -0.07$, $P = 0.77$; fathers: $r_{20} = 0.30$, $P = 0.18$).

Do Parents Favour the Same Offspring?

In trials of sons versus daughters, bluebird parents were significantly more likely to favour the same offspring; in 70% of the trials, both parents preferred the same offspring (chi-square test: $\chi^2_{1,27} = 4.48$, $P = 0.03$). Sample sizes were much smaller for the test of brighter versus duller sons, and in only 10 trials did both parents show a preference. Parents were not significantly more likely to favour the same offspring ($\chi^2_{1,10} = 1.60$, $P = 0.21$); however, in 70% of the trials, they preferred the same son.

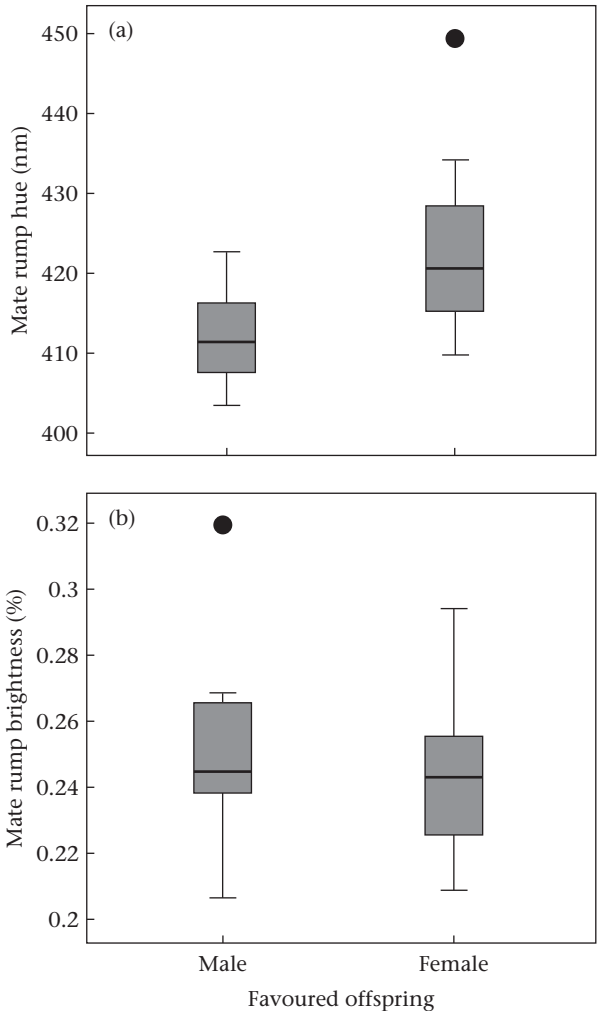

Figure 2. Likelihood that male eastern bluebirds mated to more highly ornamented females, based on (a) rump hue and (b) rump brightness, would defend their male offspring. The line within each box represents the median; the upper and lower borders of each box represent the 25th and 75th percentiles; the lower and upper bars are the 10th and 90th percentiles.

DISCUSSION

Parental Favouritism for Brighter versus Duller Males

Overall fathers showed favouritism when presented with two sons of fledgling age in the face of a simulated nest predator. Among the fathers that showed a clear preference for one son, fathers were more likely to act protectively towards brighter sons. Because we experimentally manipulated the plumage coloration of offspring, we are confident that fathers used feather coloration to discriminate between sons. Our results corroborate research indicating that honest signalling of nestling quality can influence parental favouritism, but most research has focused on how nestling mouth coloration influences parental provisioning (e.g. de Ayala et al. 2007; Ewen et. al. 2008). As plumage ornamentation in juvenile

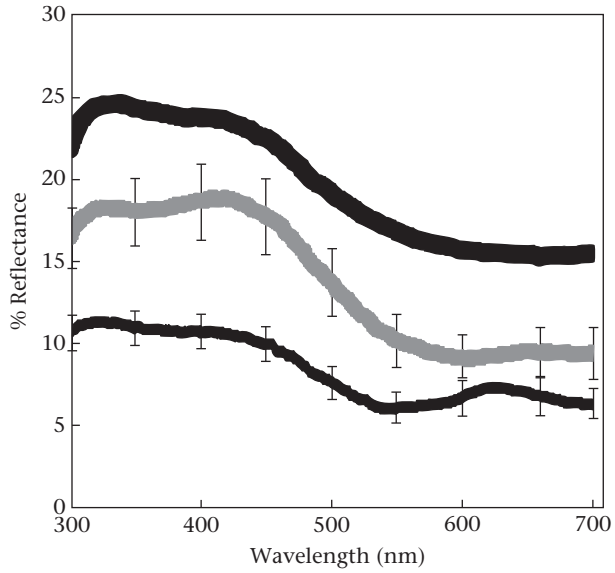

Figure 3. Reflectance curves of the wing plumage of male bluebird nestlings (1) after being experimentally brightened (thick grey line), (2) after being experimentally dulled (thin black line) and (3) prior to experimental manipulation (thick black line).

birds is relatively rare, few studies have focused on how variation in plumage coloration can signal offspring quality. There is some evidence that great tit, *Parus major*, and rock sparrow, *Petronia petronia*, parents preferentially provision nestlings with experimentally intensified carotenoid-based plumage coloration (Galvan et al. 2008; Tanner & Richner 2008; but see Tschirren et al. 2005). Moreover, in eastern bluebirds, parents bias feedings towards nestlings with experimentally intensified, structurally based blue coloration (Ligon & Hill 2010a).

Our results suggest that variation in coloration of male bluebird nestlings functions as a signal to parents. Indeed, the plumage coloration of nestling bluebirds has been demonstrated to be a condition-dependent trait; nestlings reared in crowded conditions are fed less often and grow duller blue plumage than nestlings reared in smaller broods (Siefferman & Hill 2007). Thus, the parental favouritism demonstrated in our study and in those of Ligon & Hill (2010a) are in accordance with the prediction that

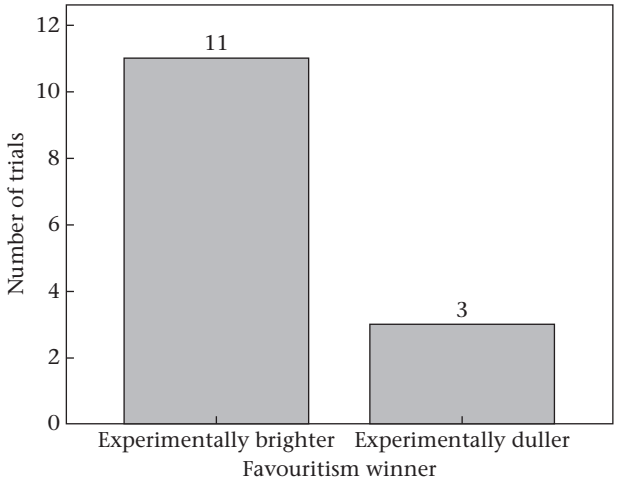

Figure 4. Number of trials during which male adult bluebirds spent the majority of their time defending their experimentally brightened and experimentally dulled male offspring.

parents should perceive the more ornamented fledglings as being of higher quality than their duller brothers. Thus, it is conceivable that parents could preferentially feed particular offspring early in the nestling stage, leading to higher body condition and brighter plumage coloration for fledglings. Brighter male bluebirds achieve higher reproductive success than do their duller counterparts (Siefferman & Hill 2003), and they may also sire more extrapair young (Gowaty & Karlin 1984). Indeed, in the sister species, the mountain bluebird, *Sialia currucoides*, more colourful males sire more offspring both in their mate's brood and in broods of extrapair mates (Balenger et al. 2009).

Parental Favouritism for Male versus Female Offspring

Eastern bluebird mothers and fathers showed favouritism towards one sibling in the gender trials, but only in fathers did these preferences appear to be influenced by the quality of their mate. Consistent with the concept that highly ornamented mates are high-quality mates, fathers that were mated to highly ornamented females showed favouritism towards sons. Male bluebirds should perceive highly ornamented females as better mates, because these females provision offspring more often, produce larger fledglings and experience higher reproductive success (Siefferman & Hill 2005a). Moreover, a quantitative genetic study found that the blue coloration of eastern bluebirds is a heritable trait (L. Siefferman, unpublished data); thus, a more highly ornamented mother should produce more highly ornamented sons. Likewise, the sons of highly ornamented females should be more reproductively valuable to their fathers. Male bluebirds mated to highly ornamented females may perceive the nest bout as being of higher-than-average quality and this should increase the likelihood that they favour sons over daughters.

To date, only three empirical studies have found parental preferences for offspring sex (Gowaty & Droge 1991; Ligon & Hill 2010b; Mainwaring et al. 2011), and other studies have failed to find support (Teather 1992; Leonard et al. 1994; Michler et al. 2010). Our results are consistent with the concept that sons are more valuable in high-quality nesting environments. Moreover, our results are similar to those of Ligon & Hill (2010b), who used a similar design but measured provisioning of offspring to test for parental preferences towards offspring sex in relation to parent coloration. In that study, fathers were more likely to provision sons when mated to more highly ornamented females and mothers were more likely to favour sons when mated to brighter males. An alternative evolutionary hypothesis for offspring sex preferences, however, is that parents favour offspring of the opposite sex to avoid future competition for breeding resources (Lessels 2002). Gowaty & Droge (1991) studied eastern bluebirds and found that fathers fed nestling daughters more often than sons, but this study may have been confounded by nestling size and behaviour. In a well-controlled experiment, zebra finch, *Taeniopygia guttata*, mothers fed sons more often than they did daughters (Mainwaring et al. 2011).

Fathers, But Not Mothers, Showed Favouritism Towards Valuable Offspring

In both experimental trials, only fathers showed evidence of favouritism towards the offspring with the highest reproductive value. Our results support the hypothesis that the sex that invests the least in the reproductive bout is more likely to favour the most valuable offspring (Lessels 2002). Indeed, differences in favouritism between mothers and fathers have been demonstrated in multiple bird species with biparental care. Males tend to favour larger or stronger offspring (Bengtsson & Ryden 1983; Slagsvold et al. 1994; Budden & Beissinger 2009; Shiao et al. 2009) while females tend to

be less likely to discriminate between offspring (Bengtsson & Ryden 1983; Gottlander 1987; Sasvari 1990; Slagsvold 1997; Kolliker et al. 1998; Krebs & Magrath 2000; Whittingham et al. 2003; Budden & Beissinger 2009; Shiao et al. 2009). In bluebirds, a reproductive bout is likely to be more energetically costly for females than it is for males; females lay eggs, incubate the eggs, brood hatchlings and provide ~50% of nestling care. Indeed, in this species, a manipulation of brood size demonstrated that females were more willing than males to increase provisioning rates to nestlings in attempt to keep up with the brood's need for food (Siefferman & Hill 2008). If females are more willing to sacrifice future reproductive effort for current reproductive effort, they may be less willing to discriminate among their offspring. Indeed, male eastern bluebirds provision the brightest offspring more often, while the conditions under which mothers discriminate among sons is much more subtle and complex (Ligon & Hill 2010a). Our results differ from those of Ligon & Hill (2010b), who found that male and female parents that were mated to highly ornamented mates provisioned sons more often than they did daughters. Another difference was that fathers' preferences for offspring sex were influenced by their mates' rusty breast coloration and not by their mates' blue rump coloration (Ligon & Hill 2010b). Our results may differ because we studied bluebirds in different geographical areas or because we measured different aspects of parental care.

We propose two alternative explanations for why males in our bluebird population may be more inclined than females to preferentially defend their more valuable offspring. Bluebirds produce more than one brood during the breeding season; as the female prepares to produce the next brood, the male assumes primary care of the fledglings (Gowaty 1983). Therefore, males invest more time and energy in offspring protective behaviours during the fledgling stage. So, fathers may experience more selective pressure to discriminate among fledglings than do mothers. However, sensory bias may also influence male behaviour. Although the blue coloration of adult male bluebirds appears to be a sexually selected trait, it is not driven by female choice for brighter males (Liu et al. 2007); instead, plumage coloration functions in male–male competitive interactions (Siefferman & Hill 2005b; Mercadante 2010). So we speculate that fathers could be more responsive to variation in plumage coloration than mothers. This could also explain why fathers adjusted parental care in relation to mate ornamentation while mothers did not.

While only fathers demonstrated preferences for the offspring of the most valuable sex, mothers and fathers were significantly more likely to choose the same offspring than would be expected by chance. This pattern was also found in rock sparrows (Griggio et al. 2009), the only other study that we know of that measured parental care favouritism via parental defence behaviours. These results suggest that the aggressive behaviour of one parent may influence the other. Unfortunately, we were unable to determine which parent was copying the other. Furthermore, our initial attempts to remove one parent during the trials caused the remaining parent to become preoccupied with calling for and searching for the missing mate. However, four lines of evidence suggest that females may copy males. First, males showed favouritism in both experiments, while females did not. Second, male bluebirds are more aggressive than females and spend more time defending the territory than do females (Gowaty & Plissner 1998). Third, fathers are the primary caregivers for fledgling-aged birds. Fourth, Ligon & Hill (2010a) found that female feeding decisions towards nestlings were statistically similar to the feeding decisions of fathers, suggesting that females may follow the lead of their mates. If, indeed, the mother's behaviour is influenced by that of her mate, it may explain why we were unable to detect an effect of offspring sex or colour on mothers' preferences.

We have shown that eastern bluebird fathers preferentially defend their higher-quality offspring during the fledgling period. Because male and female offspring are dichromatic by age 13 days, it is likely that fathers also use variation in plumage colour to discriminate between sons and daughters. Future work should focus on determining why parents vary in the likelihood of showing favouritism and the long-term consequences of favouritism for both parents and offspring.

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