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PEEK-A-BOO, WHERE ARE YOU? THE SEXUAL CONFLICT UNDERLYING
BEHAVIOURAL COMPENSATION IN A SONGBIRD WITH BIPARENTAL CARE

by

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PREFACE

The Bowers lab has many biological areas of interest to study which include, behaviour, evolution, physiology, and ecology. Of course, however diverse our interests are, every member of the lab has a passion for discovery of new ideas through the scientific method. The research in this study was founded upon behavioural research that underlies the reasoning behind sexual conflict and behavioural compensation to explain a possible mechanism in which one parent in a bi-parental species may compensate for their partner's level of care. This co-authored manuscript has been submitted for publication and has been formatted in the style of the journal *Animal Behaviour* to which it has been submitted. All research activities were performed in accordance with the Illinois State University Institutional Animal Care and Use Committee (Protocol No. 04-2013) and United States Geological Survey banding permit 09211.

ABSTRACT

In any family, conflict between care-givers arises over how much to invest in their shared genetic kin. We examined this conflict in a wild population of house wrens (*Troglodytes aedon*), recording parental behaviour twice for each nest monitoring shifts with nestling age, assessing female response to male behaviour and nestling begging. Early in nestling development, maternal provisioning was responsive to male provisioning but not nestling begging. Later in development, females increased the frequency of provisioning and inspecting her surroundings with both the reduction of male provisioning and increases in begging; resulting in less time brooding which delayed fledging age. Males that provisioned more were less likely to breed the next year. Our data suggest that sexual conflict elicits changes in female care through direct observation of their mate, but that the multimodal nature of care and division of labour between mates may necessitate a reassessment of conflict over biparental care.

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CHAPTER 1

**Peek-a-boo, where are you? The sexual conflict underlying
behavioural compensation in a songbird with biparental care**

Jonathan B. Jenkins

In any family, conflict between care-givers arises over how much to invest in their shared genetic kin. How is the extent of this conflict assessed by each parent? Does either parent monitor the other's behaviour? We asked these questions in an observational study of nestling begging and parental provisioning in a wild population of house wrens (*Troglodytes aedon*), a cavity-nesting songbird, over two breeding seasons. We recorded parental behaviour twice for each nest to monitor shifts with nestling age, assessing how females in particular responded to their mate's provisioning and nestling begging solicitations. Early in the nestling period, maternal care was responsive to male provisioning but not to nestling begging. However, a few days later, both nestling begging and paternal care affected maternal behaviour, including her provisioning rate and the frequency with which she peered outside her nest cavity (a nestbox) while brooding to visually inspect her surroundings. Females increased the frequency of these behaviours with reductions in male provisioning and increases in nestling begging. When males provisioned little or no food, females spent more time peeking out of the nestbox, and, if the male did not show up, compensated by provisioning more food herself. Consequentially, the less a male provisioned, the less time females spent brooding their young, which prolonged nestling development and delayed fledging age. Males provisioning more were less likely to return to breed in subsequent years, suggesting an optimal level of investment for males; however, provisioning effort did not affect the return of females. Our data suggest that sexual conflict elicits changes in female care through direct observation of their mate, but that the multimodal nature of care and division of labour between mates, namely when one sex provides a form of care the other does not, may necessitate a reassessment of conflict over biparental care.

Keywords: cost of reproduction, parent-offspring conflict, parental care, sexual conflict

To maximize fitness, individuals must strike an optimal balance between the costs and benefits of investing into current reproductive effort. With respect to parental investment, life-history theory predicts that, if individuals have sufficient residual reproduction value, then limiting resources should induce a trade-off between current reproductive effort and the self-maintenance necessary to ensure their own survival and future reproduction (Williams, 1966; Trivers, 1973; Stearns, 1992; Bowers et al., 2012; Hodges et al., 2015; Fowler & Williams, 2015, 2017). Participation in a pair bond may increase one's fitness, but family life introduces various conflicts, including sexual conflict over biparental care and parent-offspring conflict over how much care to provide any given offspring (Trivers, 1972, 1974; Smith & Fretwell, 1974; Mock & Parker, 1997; Parker et al., 2002; Royle et al., 2002a). Offspring may solicit more care than their parents have been selected to provide, as increasing levels of care should enhance survival prospects of individual young, but this can reduce the parents' ability to invest in other offspring, thereby lowering the parents' inclusive fitness (Trivers, 1974; Smith & Fretwell, 1974; Parker et. al., 2002).

In the context of biparental care, sexual conflict arises when the reproductive strategy pursued by one parent increases its own fitness while reducing the fitness of its partner (Parker, 1979). In most animal taxa, reproductive success of males varies directly with their number of mates, whereas reproductive success of females is constrained by the number of eggs they produce and not by the number of males with which they mate (Bateman, 1948). Thus, male fitness may be maximized by pursuing additional mates instead of providing parental care (Maynard Smith, 1977; Queller, 1997; see also Székely & Cuthill, 2000), forcing females to provide a greater level of parental care than would

be expected given their genetic contribution to the brood (Westneat & Sargent, 1996; Houston et al., 2005). Even in socially monogamous species, males also reap comparatively fewer benefits from providing parental care because they generally have a lower relatedness to the brood as a consequence of extra-pair copulations by the female (Westneat & Sherman, 1993; Westneat & Sargent, 1996; Queller, 1997; Matysioková & Remeš, 2013). Possibly because of this lower relatedness, paternal care often increases more strongly than maternal care with increasing sizes of broods and offspring, because larger broods should be more likely to contain related individuals (Moreno et al., 1995; Leonard & Horn, 1996; Smiseth & Moore, 2004; Westneat et al., 2011; Low et al., 2012; but see also Wright & Cuthill, 1990).

Much of how parents in biparental species cooperate and respond to their partner's level of care for shared offspring remains unknown (Houston et al., 2005). A plausible explanation for the wide diversity of parental responses is a model known as the 'negotiation continuum', in which one parent physically responds to the behaviour of the other (McNamara et al., 1999; Schwagmeyer et al., 2002; Hinde, 2006; Johnstone & Hinde, 2006). This continuum ranges from individuals expressing a fixed level of care regardless of what their mate does (Houston & Davies, 1985; Lozano & Lemon, 1996; Schwagmeyer et al., 2002; Nakagawa et al., 2007) to those that respond positively or negatively to their mate's level of care (Wright & Cuthill, 1989, 1990; Wright & Dingemanse, 1999; Sanz et al., 2000; Smiseth & Moore, 2004; Hinde & Kilner, 2007; Nakagawa et al., 2007; Harrison et al., 2009; Westneat et al., 2011). Instances in which brood size affects provisioning may, thus, constitute a strategy on the negotiation continuum between parents. It is important to note, however, that parental negotiation

assumes that each caregiver has precise information on how much care their partner is contributing, which may be observed directly or inferred indirectly through nestling begging and condition (Wright & Dingemanse, 1999; Schwagmeyer et al., 2002).

However, it is not always clear that either parent actually has this knowledge, and, if so, responds with expected changes in food provisioning. Indeed, instances in which the behaviour of care-giving parents appears consistent with compensation and negotiation might not reflect a direct response to the behaviour of their partner, but may simply be a response to nestling begging solicitations (Wright & Dingemanse, 1999), without requiring any knowledge of what their partner is doing.

In this study, we monitored the parental behaviours of the house wren (*Troglodytes aedon*) in the contexts of sexual conflict and parent-offspring conflict. Both males and females are single-load provisioners, bringing only a single arthropod to the nest at each feeding (Greenewalt & Jones, 1955; Barnett et al., 2012). Typically, males deliver food to the female while the female is brooding the young, which she then passes to offspring, although males will enter the nest cavity to deliver the food directly when females are not brooding. In fact, brooding females routinely perch at the entrance to the nestbox and poke their head out to visually inspect or scan their surroundings (Fig. 1), and we suspect this is induced by the tardy males' prolonged duration between food deliveries, inducing a potential trade-off between brooding and provisioning within females (e.g. Johnson & Best, 1982). Thus, brooding females may be well-positioned to gauge their mate's attentiveness and provisioning effort, with the number of trips to the nest, with a single prey item, providing a reliable proxy for the amount of food he delivers, and potentially adjust their own behaviour in response. We suspect that females'

expectations of males are exacerbated when their offspring are hungry. In other words, nestling begging should promote provisioning, but reduced provisioning by males may lead females to inspect their surroundings and to reduce brooding and increase foraging to satiate the brood. Thus, we tested whether multiple components of maternal behaviour (i.e. food provisioning, inspection of surroundings outside the nest, and time spent brooding) respond to (1) male provisioning effort, and (2) nestling begging vocalizations, predicated on females actively taking notice of male provisioning effort. Specifically, we predicted that a male's provisioning rate would be negatively associated with the frequency with which his mate visually scanned her surroundings and foraged to find food for their young, and that increased nestling begging would amplify these behaviours.

METHODS

Study Species and Site

House wrens are small (10-12g), insectivorous, secondary cavity-nesting songbirds with a wide breeding distribution. The migratory northern subspecies (*T. aedon aedon*) breeds across the middle section of eastern North America, spanning from the Atlantic to the Pacific from the southern end of the Appalachian range north to southern Maine (biology summarized in Johnson, 2014). Females usually select a mate that is defending a nesting site and has built a base of a nest with sticks inside the nest cavity; nest construction is then completed by the female with feathers, grasses, and other soft materials (Finke et al., 1987; Dobbs et al., 2006). Females in the study population produce a modal clutch size of seven eggs for the first brood of a breeding season and six eggs if an additional breeding attempt is made in the same season (Finke et al., 1987; Dobbs et al., 2006). Only the

female incubates eggs and broods young nestlings, brooding until the young are eight to ten days of age and have begun to thermoregulate for themselves (Dunn 1976). Both parents provision young upon hatching, and males deliver food to brooding females, which is generally transferred to nestlings, early in the nestling stage (Bowers et al., 2014b); the length of the nestling period is 15 days, on average (Bowers et al., 2013).

As obligate cavity-nesters, house wrens readily accept nestboxes as nesting sites. Our study site, with a box-nesting population, was located in secondary deciduous forest in McLean County, Illinois, USA (40.665°N, 88.89°W). Nestboxes were distributed on a 30-m × 60-m grid, and were placed atop 48.3-cm diameter aluminium predator baffles on 1.5-m poles. Lambrechts et al. (2010) provide further details on nestboxes.

Procedures

Once adults had established nests and were approximately half-way through incubation, we caught them by utilizing a trap door at the entrance of the nestbox or mist nets placed next to the box. We banded adults with a uniquely numbered United States Geological Survey leg band. Males were given three additional coloured bands (a total of two bands per leg), which we arranged in unique combinations to easily identify each male without having to recapture them.

We monitored parental behaviour twice during the breeding cycle in the 2014 and 2015 breeding seasons (May-August). Our sample of nests in this study ($N = 97$ nests) was part of a larger manipulative experiment involving food-supplementation of nestlings, and our observations here are focused on non-experimental nests from that study. We monitored nestling begging and parental provisioning on two days: first at 4 d

posthatching (or occasionally on the 5th day if inclement weather precluded an observation of sufficient length the day before) and again 7 d posthatching. We recorded nestling begging vocalizations using a small microphone within nests attached to a digital voice recorder outside the nest (Barnett et al., 2011; Bowers et al., 2016), and we counted these vocalizations using Raven Pro 1.5 (Cornell Lab of Ornithology). This allowed us to target begging calls specifically and count the number of vocalizations efficiently and accurately in an automated fashion (for further details see Bowers et al., 2016, Bowers et al., in review). We also filmed food provisioning to nests using a Kodak Zx1 or Zx5 video cameras mounted in a sheath on a 1.5-m pole ca. 1-2 m from the nestbox. Poles and a dummy camera were established 24 h prior to filming to allow parents time to habituate to the presence of the camera (Barnett et al., 2012; Sakaluk et al., 2018). Cameras generally recorded for 100-120 minutes to allow for at least a full hour of observation time, which provides a sufficiently representative sample of consistent individual differences in behaviour (Murphy et al., 2015). After videos were obtained, we analysed 60 min of each video starting when a parent first returned to the nestbox (usually in less than 5 min), scoring them based on observed behaviours (e.g. number of provisioning trips, male singing, and females peering out of nestboxes).

Data and Analysis

All analyses were conducted using SAS (version 9.4), with two-tailed hypothesis tests ($\alpha = 0.05$). All figures displaying raw data include light dots depicting individual data; darkened dots represent overlapping data. First, we analysed multi-modal maternal behaviour (food provisioning, number of times females inspected their nestbox

surroundings by peering out the nestbox entrance, and the time females spent brooding during our hour-long observations) in relation to nestling begging frequency and paternal behaviour (frequency of male provisioning and singing near the nestbox) with a multivariate analysis of variance (MANOVA; PROC GLM) on both day 4/5 and on day 7 posthatching. As a follow-up, we calculated Pearson's correlation coefficients to depict the strength of relationships between a given pair of dependent and independent variables as a measure of effect size (Figs. 2,3; Rosenthal, 1994). We then assessed consequences of parental care on offspring, including effects of parental care on pre-fledging body mass, fledging age, and offspring recruitment as breeding adults in subsequent years. Nestling body mass was analysed in relation to total female provisioning and brooding, and total male provisioning (i.e. the sum of provisioning trips and brooding time across the two, hour-long observations) using a linear mixed model with maternal identity and year as random effects to account for non-independence of young produced by the same female and within years. We assessed offspring recruitment using a similar approach, except using a generalized linear mixed model with a Poisson distribution to analyse the number of recruits produced (most pairs produced zero recruits). We analysed fledging age using a similar approach, assuming a normal distribution, in relation to total maternal care and paternal provisioning. Finally, we analysed parental return rates to determine how provisioning rates might influence parents' returning to breed in the population in subsequent years using a generalized linear mixed model with a binary response (returned or did not return), and we controlled in this analysis for the number of young fledged, as return rates of parents often vary with breeding success (Greenwood & Harvey, 1982; Drilling & Thompson, 1988).

Ethical Note

House wrens are tolerant of human activity at their nest, including the capturing and measuring of adults and their young once females are several days into incubation. Nonetheless, we attempted to minimise disturbances to breeding pairs during the nesting cycle through various means, including (1) delaying the capture of adults until ca. halfway through incubation (or later) to avoid maternal abandonment, (2) colour banding adult males so we did not have to retrap them in mist nets to identify them subsequently, and (3) minimising as much as possible the time spent setting up cameras and recorders for our behavioural observations. All research activities were performed in accordance with the Illinois State University Institutional Animal Care and Use Committee (Protocol No. 04-2013) and United States Geological Survey banding permit 09211.

RESULTS

Parental Responses to Social Mates and Offspring

Females peered out of their nestbox and inspected the surrounding area at both 4/5 and 7 d posthatching, but the frequency with which they did this differed for the different nestling ages (Figs. 2,3). On day 4/5, male provisioning rate had a weak effect on multivariate maternal care (i.e. maternal provisioning, peering from the nestbox, and time spent brooding; Table 1A). Although male provisioning rate affected maternal provisioning rate and time spent brooding (Table 1A; Fig. 2A,C), there was no correlation between male provisioning rate and the number of times females peered from their nestbox (Table 1A; Fig. 2B). There was, however, a marginally non-significant

tendency for increased male singing frequency to reduce the propensity of females to peer from their nestbox to inspect their surroundings (Table 1A; $r = -0.159$), and increases in singing frequency were associated with increased provisioning rates within males ($r_{94} = 0.362$, $P < 0.001$). Nestling begging vocalizations, on the other hand, while tending to affect maternal provisioning, ultimately did not affect multivariate maternal care (Table 1A; Fig. 2D,E). There was, however, a correlation within females between the number of times they peered outside their nestbox and their own provisioning rate, indicating that females who peeked outside their nestbox also made more provisioning trips to feed their young (Fig. 2F). There was also a negative correlation within females between food deliveries and time spent brooding their young ($r_{95} = -0.281$, $P = 0.005$).

Both paternal provisioning and nestling begging vocalizations were associated with significant effects on maternal care on day 7 posthatching, whereas there was no effect of male singing on maternal care (Table 1B). Similar to the pattern observed on day 4/5, female provisioning on day 7 was negatively correlated with male provisioning, as a higher male provisioning rate predicted a lower female provisioning rate, although this effect was stronger at this later stage of nestling development (Fig. 3A). Male provisioning at this stage also affected the female's propensity to visually scan her surroundings while in the nestbox, whereby the frequency of this behaviour decreased as male provisioning increased (Table 1B; Fig. 3B). Additionally, the higher the provisioning rate of the male, the more time the female spent on the nest (Fig. 3C).

Although nestling begging did not predict components of maternal care earlier in development, increased nestling begging was predictive of increases in maternal food provisioning on day 7 posthatching (Table 2B; Fig. 3D). These effects are in contrast

with those of nestling begging on male provisioning, as males increased their provisioning with increases in nestling begging on day 4/5 ($r_{88} = 0.210$, $P = 0.047$), but not on day 7 ($r_{70} = 0.180$, $P = 0.129$).

Effects of Parental Care on Offspring

There was no significant effect of parental care (provisioning by either parent on day 4/5 or day 7) on nestling pre-fledging mass (all $P > 0.3$). There was, however, a tendency for increased total prey deliveries to increase the number of offspring recruited as breeding adults within the study population in future years (estimate \pm SE = 0.083 ± 0.043 , $F_{1, 79} = 3.76$, $P = 0.056$), and this was the case while controlling for variation in hatching date (estimate \pm SE = -0.052 ± 0.019 , $F_{1, 79} = 7.18$, $P = 0.009$) and brood size at fledging (estimate \pm SE = -0.095 ± 0.188 , $F_{1, 79} = 0.25$, $P = 0.616$). The effect of food provisioning overall was manifest primarily as a strong effect of maternal provisioning (estimate \pm SE = 0.119 ± 0.037 , $F_{1, 80} = 10.36$, $P = 0.002$), with no effect of paternal provisioning (estimate \pm SE = -0.066 ± 0.062 , $F_{1, 80} = 1.13$, $P = 0.290$). Fledging age was similarly affected by both maternal food deliveries and time spent on the nest brooding young, with increases in maternal provisioning and brooding time acting to advance fledging age (effect of total maternal food delivery: estimate \pm SE = -0.049 ± 0.021 , $F_{1, 63} = 5.43$, $P = 0.023$, Fig. 4A; effect of total maternal brooding time: estimate \pm SE = -0.016 ± 0.008 , $F_{1, 63} = 4.27$, $P = 0.043$, Fig. 4B), while controlling for variation in paternal provisioning (estimate \pm SE = -0.018 ± 0.019 , $F_{1, 63} = 0.94$, $P = 0.337$).

Costs of Parental Care

There were no negative effects of increasing maternal care on day 4/5 posthatching on the probability that a female would produce multiple broods of young within a given breeding season (maternal provisioning: $F_{1,68.4} = 0.35$, $P = 0.557$; peering from the nestbox: $F_{1,69} = 0.93$, $P = 0.337$; paternal provisioning: $F_{1,69} = 1.40$, $P = 0.241$), although there was a nonsignificant tendency for females that spent more time brooding their young to have an increased likelihood of producing a second brood later the same breeding season (estimate \pm SE = 0.041 ± 0.021 , $F_{1,69} = 3.80$, $P = 0.055$). On the other hand, the frequency with which females visually inspected their surroundings while on the nest on day 7 posthatching negatively predicted whether or not they would produce a second brood. That is, females that peered from their nestbox more frequently were less likely to produce a second brood (estimate \pm SE = -0.136 ± 0.062 , $F_{1,57} = 4.82$, $P = 0.032$), but no other components of parental care on day 7 were significant (maternal provisioning: $F_{1,56.63} = 0.63$, $P = 0.430$; maternal brooding time: $F_{1,53.92} = 0.13$, $P = 0.717$; paternal provisioning: $F_{1,57} = 3.38$, $P = 0.071$).

The probability that a female would return to breed within the population in subsequent years was not affected by her total provisioning rate (i.e. combined provisioning rates on day 4/5 and on day 7; $F_{1,64} = 0.03$, $P = 0.866$), by male provisioning rate ($F_{1,64} = 0.46$, $P = 0.502$), the number of young fledged ($F_{1,64} = 0.58$, $P = 0.448$), or components of parental care on day 4/5 or day 7 (all $P > 0.05$). However, while maternal provisioning rate did not affect whether her mate returned to breed in subsequent years ($F_{1,59} = 1.32$, $P = 0.256$), the return rate of males was negatively affected by their own total provisioning rate (estimate \pm SE = -0.103 ± 0.043 , $F_{1,59} = 5.88$, $P = 0.018$; Fig. 5). Males fledging more young per brood within a year were also

more likely to return to breed in future years (estimate \pm SE = 0.780 ± 0.274 , $F_{1, 59} = 8.08$, $P = 0.006$).

DISCUSSION

Although family life may increase an individual's inclusive fitness, each group member has its own fitness interests that might be expected to lead to conflict between males and females over the amount of care either of them provides, as well as to conflict between offspring and their parents over how much care the offspring receive. These conflicts arise when the optimal level of care for fitness maximization differs between male and female parents and between parents and their offspring, as offspring are generally expected to solicit more care than their parents have been selected to provide (Trivers, 1974; Parker, et al., 2002).

Sexual Conflict

The question of how parents might respond to their partner's level of care has attracted significant attention from researchers over recent decades, but we still have an incomplete understanding of the origin and maintenance of diversity in these responses (Houston et al., 2005; Westneat et al., 2011). Although, it is not always clear whether, or how, either parent actually monitors the food delivered by their partner, our study reveals a novel mechanism through which this could occur, particularly when ectothermic young require an exogenous source of heat provided by brooding parents. Although some proportion of peering from the nestbox and scanning their surroundings may involve vigilance for nest predators, females are actually no more likely to do this when the

potential for nest depredation is experimentally increased (Dorset et al., 2017), and we found that females most often peered from their nestbox and visually scanned the surrounding area when their partner was providing little, or no, food for their nestlings. This simple behavioural response suggests that females notice that males have lowered or ceased provisioning, and we propose that when females are peering from their nestbox they are largely inspecting the area either for their mate or, possibly, for a prey item that can be easily obtained. Either way, this behaviour suggests that compensatory increases in provisioning by the female is indeed a direct response to the male's behaviour. In other words, for a female to adjust her provisioning and brooding behaviour in the absence of her mate, she would have to observe that he was not provisioning.

The behavioural responses by parents to partner effort have typically taken on the form of compensation, with one parent offsetting (often incompletely) a reduction in care from their partner with increases in the amount of care they provide (Harrison et al., 2009); however, positive associations between levels of care provided by members of a breeding pair have also been reported (Hinde, 2006; Westneat et al., 2011). We found that, on day 7 posthatching, females were especially responsive to changes in male food provisioning, largely in a compensatory manner. Reduced food provisioning by males was most often associated with increases in provisioning by females and a greater frequency of females peering from their nestboxes while brooding to inspect their surroundings, while increased male provisioning predicted an increase in the amount of time females spent on the nest brooding their young, as was also observed in Will et al. (2017). When viewed separately, the responses of females in terms of food provisioning could be taken as evidence for compensation, but brooding of young is also a critical

form of postnatal care that enhances nestling growth (e.g. Bowers et al., 2015a; Mueller et al., in review), and the amount of time females spent doing this varied positively with male provisioning, suggesting a positive response to increases in care from their partner. Similarly, Markman et al. (1995) observed a compensatory increase in paternal provisioning when maternal provisioning was experimentally reduced, but this necessitated that these males spend less time guarding their nest, another critical form of parental care that may trade off with provisioning effort within individuals. Indeed, parental care is multi-modal, yet a large majority of studies investigating parental negotiation centre around a single form of care, namely, food delivery (but for exceptions see, e.g. Markman et al., 1995; Nakagawa et al., 2007; Trnka & Grim, 2013). Our understanding of sexual conflict will be incomplete until we consider multi-modal parental care and the division of labour that commonly exists in biparental species.

Results from empirical studies of conflict over biparental care vary widely, and part of this inconsistency may be attributable, at least in part, to difficulty in obtaining consistent measures of compensation and its consequences for offspring. Most previous studies have ignored time spent on the nest brooding, which may be vital to determining if this trade-off in compensation has a lasting effect on the offspring (see also Wolf et al., 1990; Harrison et al., 2009). We detected a significantly positive correlation between male provisioning and the amount of time females spent on the nest brooding their young, and a negative correlation between male and female provisioning. Thus, when the male is absent from the nest, the female tends to provision more heavily, necessitating that she spend more time off the nest. Being off the nest not only makes the young more vulnerable to predators, including infanticidal male conspecifics, but also can potentially

prolong the period of nestling development before nestlings attain a minimum developmental threshold prior to fledging (Carrier & Auriemma, 1992; Michaud & Leonard, 2000; Bowers et al., 2015a; Mueller et al., in review). Thus, behavioural compensation may be manifest not simply by an increase in feeding rate, but ultimately in the duration of nestling care.

We might expect sexual conflict to affect not just members of a breeding pair, but their offspring as well (Royle et al., 2002b; McNamara et al., 2003). However, although we detected an effect of maternal provisioning on offspring recruitment, but no effect of paternal provisioning, it is important to note that this does not negate the importance of male care, as the more a male provisions, the more time the female can spend brooding their young. It has now been shown in a number of species that increases in the temperature of nest microclimates and the amount of time parents spend brooding their nestlings can have a positive effect on nestling body condition (Dawson et al., 2005; Bowers et al., 2015a; Mueller et al., in review; but see also Salaberria et al., 2014), a trait that is often predictive of long-term recruitment and lifetime reproductive success (Tinbergen & Boerlijst, 1990; Young, 1996; Both et al., 1999; Naef-Daenzer et al., 2001; Bowers et al., 2014a, 2015b).

Finally, we found that increases in male provisioning rate negatively affected their own probability of returning to breed in the local population in future years. Although failing to return to breed in future years may be a consequence of factors other than mortality, such as fidelity to a breeding site, this fidelity is most often affected by reproductive success, or the number of young fledged within a given year (Greenwood & Harvey, 1982; Drilling & Thompson, 1988), and we controlled for this in our analysis of

male return rates. Indeed, effects of provisioning on return rates are often observed in males, but not females (Santos & Nakagawa, 2012; Williams & Fowler, 2015). As such, the cost of providing care is generally thought to play a fundamental role in generating sexual conflict, even when males might be the genetic sire of all the young in their nest (Trivers, 1972; Bowers et al., 2014b; Fowler & Williams, 2017).

Parent-offspring Conflict

We found no effect of offspring begging on maternal care early in nestling development on day 4/5 posthatching, suggestive of parent-offspring conflict as females were not responsive to offspring begging solicitations. Both parents might be selected to respond positively to begging by increasing food provisioning, as enhancing offspring survival should augment their inclusive fitness; however, they may also be selected not to respond at all to begging insofar as this might otherwise cause them to provide a greater-than-optimal level care. Begging may indeed be a ‘psychological weapon’ (Trivers, 1974) that parents must interpret correctly (Trivers, 1974; Godfray, 1995; Mock et al., 2011; Bowers et al., in review). Here, we found that parents responded to begging solicitations by increasing provisioning rates on day 7 posthatching, a time at which females spent less time on the nest, but females did not respond to nestling begging earlier on day 4/5, when they spent more time on the nest. Begging intensity has traditionally been thought to serve as an honest signal that promotes increased feeding (Godfray, 1995; Mock et al., 2011), so this shift may reflect a greater need for parental responsiveness later in development. A resolution of what, exactly, offspring begging solicitations

communicates to parents, and whether the information encoded in their solicitations changes with age, awaits further study.

Conclusions

It is generally expected that parents should be selected to provide an optimal level of care across ecological contexts in a cost-benefit framework. Here, parents appeared less likely to respond to begging solicitations through changes in provisioning earlier in nestling development, but later on responded to nestling begging with increased provisioning. At this later stage, increases in nestling begging induced increases in both maternal food provisioning and the frequency with which she peered out of her nestbox to inspect her surroundings, and females were also more likely to do this when their mates were provisioning at a below-average rate. In the absence of the male, females generally decided to provision their nestlings rather than stay on the nest brooding them, generating a conflict between the sexes over biparental care. Our data suggest that conflict is attributable, at least in part, to a cost of increased provisioning by males to their probability of breeding in future years. The reduction in male provisioning can be ameliorated, at least partially, but increases in provisioning by females, seemingly because females have accurate information on male effort. While most research on behavioural compensation has focused directly on the provisioning of food to offspring, further work is needed to incorporate the dynamic and multi-modal behavioural responses and division of labour between parents.

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Table 1. MANOVA of maternal behaviours (food provisioning, peering from the nestbox, and time spent brooding) in relation to nestling begging frequency and male provisioning.

Effect	Pillai's trace	<i>F</i>	df	<i>P</i>	Standardized canonical coefficients:		
					Food provisioning	Peering from the nestbox	Time spent brooding
A. Day 4/5 posthatching							
Nestling begging	0.068	1.98	3, 81	0.123	1.096	-0.122	0.381
Male provisioning rate	0.102	3.06	3, 81	0.033	-0.914	0.900	0.056
Male singing	0.074	2.17	3, 81	0.099	-0.664	1.065	-0.458
B. Day 7 posthatching							
Nestling begging	0.178	4.63	3, 64	0.005	0.974	0.444	-0.094
Male provisioning rate	0.265	7.68	3, 64	< 0.001	0.754	0.464	-0.458
Male singing	0.055	1.23	3, 64	0.306	0.557	0.658	-0.494



Figure 1. A female visually inspecting the environment around her nestbox while perched inside the entrance (photo credit: Dylan Poorboy, used with permission).

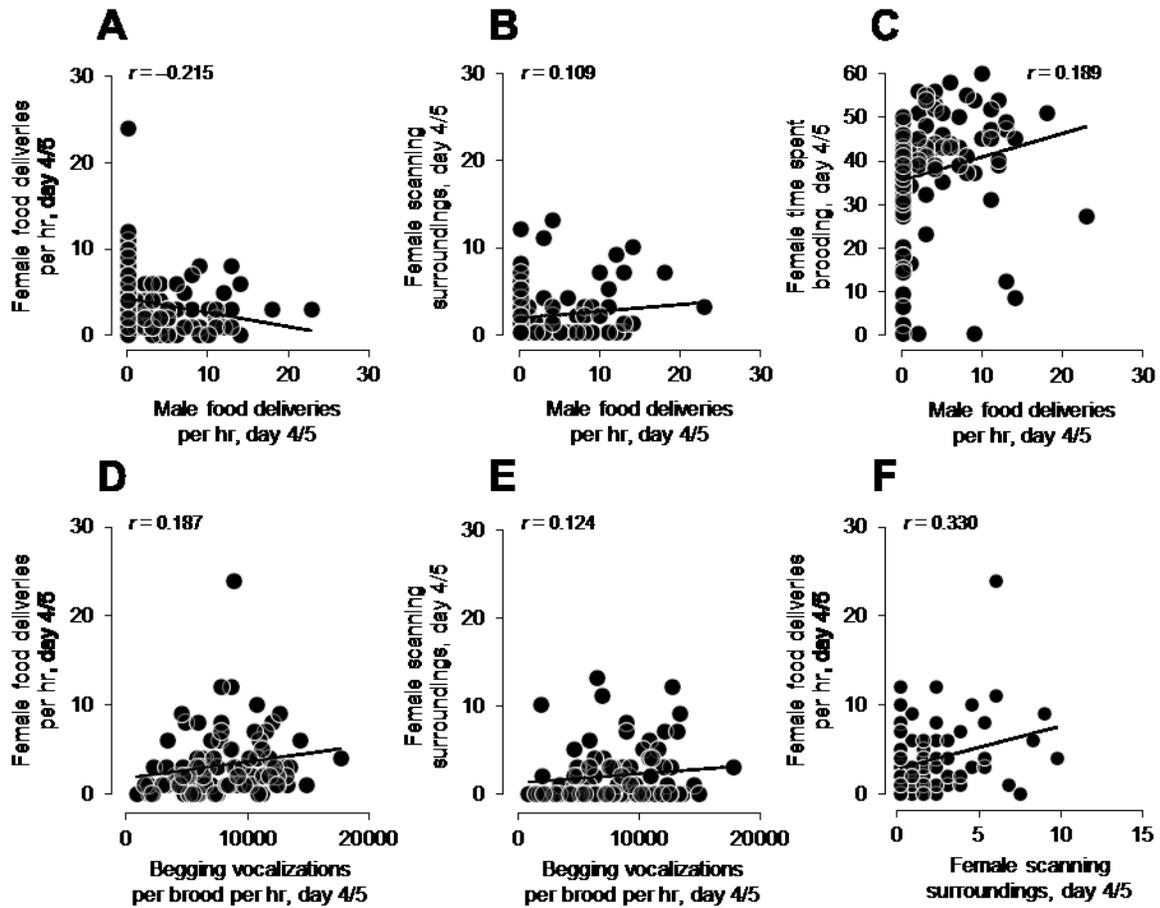


Figure 2. Associations on day 4/5 posthatching between maternal food provisioning, the frequency of peering from the nestbox, and time spent brooding during our observation in relation to male food deliveries (A-C), nestling begging vocalizations (D,E), and the relationship between food provisioning and peering from the nestbox within an individual (F).

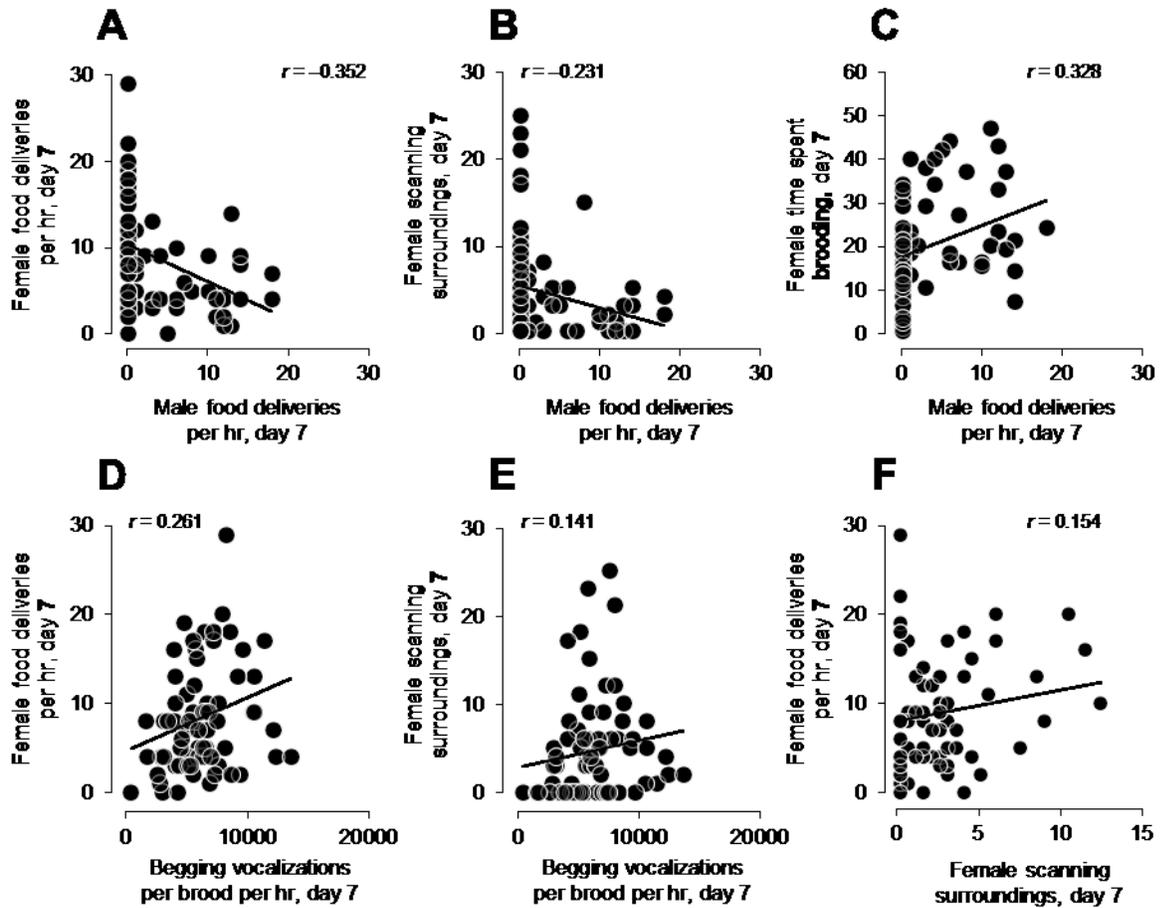


Figure 3. Associations on day 7 posthatching between maternal food provisioning, the frequency of peering from the nestbox, and time spent brooding during our observation in relation to male food deliveries (A-C), nestling begging vocalizations (D,E), and the relationship between food provisioning and peering from the nestbox within an individual (F).

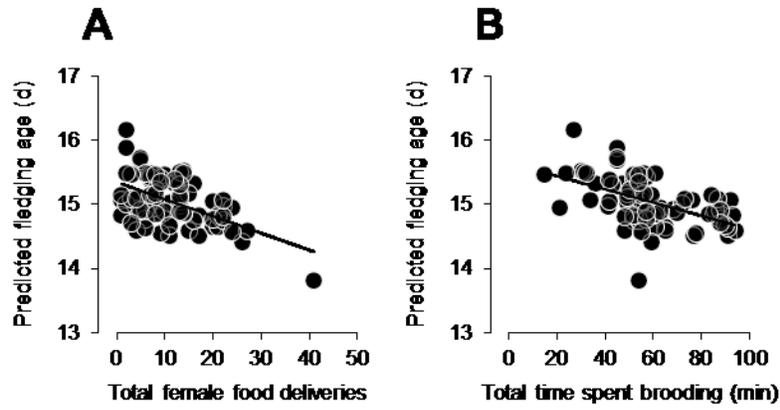


Figure 4. Predicted age at fledging in relation to (A) total maternal food deliveries, and (B) total maternal brooding time, both summed across the two, hour-long observations of parental behaviour. The predicted ages are from a linear model that also controlled for paternal provisioning rate.

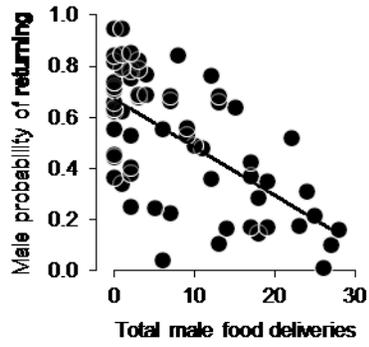


Figure 5. Predicted probability of a male returning to breed within the population in subsequent years. Predicted values are from a generalized linear model simultaneously controlling for maternal provisioning and fledging success.

Highlights

- Females rearing young monitor, and respond to, levels of care provided by their mate.
- Female care corresponded to nestling begging later, but not earlier, in development.
- Maternal care involved a trade-off between feeding and brooding shaped by male care.
- Reduced male provisioning meant less time females spent brooding their young.
- Males provisioning more food were less likely to breed in future years.