



Female birds monitor the activity of their mates while brooding nest-bound young

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Abstract

In addition to food and protection, altricial young in many species are ectothermic and require that endothermic parents provide warmth to foster growth, yet only one parent – typically the female – broods these young to keep them warm. When this occurs, reduced provisioning by males obliges females to forage instead of providing warmth for offspring, favoring the temporal mapping of male activities. We assessed this in a wild house wren population while experimentally feeding nestlings to control offspring satiety. While brooding, females look out from the nest to inspect their surroundings, and we hypothesized that this helps determine if their mate is nearby and likely to deliver food to the brood (males pass food to brooding females, which pass the food to nestlings). Females looked out from the nest less often when their partner was singing nearby and when his singing and provisioning were temporally linked, signaling his impending food delivery. Females also left to forage less often when their mate was nearby and likely to deliver food.

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Nestling begging did not affect these behaviors. Females looking out from the nest more often also provisioned at a higher rate and were more likely to divorce and find a new mate prior to nesting again within seasons, as expected if females switch mates when a male fails to meet expectations. Our results suggest anticipatory effects generated by male behavior and that brooding females temporally map male activity to inform decisions about whether to continue brooding or to leave the nest to forage.

Keywords

Classical conditioning; Cost of reproduction; Parent-offspring conflict; Parental care; Sexual conflict; Temporal mapping

Introduction

Although participation in a pair bond may increase one's fitness, family life introduces various conflicts, including a sexual conflict over biparental care in which the reproductive strategy pursued by one parent increases its own fitness while reducing the fitness of its partner (Trivers 1972; Parker 1979; Kokko and Jennions 2008). In most animals, male reproductive success varies directly with their number of mates, whereas female reproductive success is constrained principally by the number of eggs produced (Bateman 1948; Kokko et al. 2006; Fromhage and Jennions 2016). Thus, although there could be instances in which providing care has a greater effect on male fitness (e.g., Kokko and Jennions 2008), in many circumstances, male fitness may be maximized by pursuing additional mates instead of providing parental care (Maynard Smith 1977; Queller 1997; Székely and Cuthill 2000), thereby forcing females to provide an unequal, heightened level of care than would be expected given their genetic representation within the brood (Westneat and Sargent 1996; Houston et al. 2005).

Although the relative contribution of each sex toward parental care has received a high degree of research interest in recent years, much of how parents in biparental species cooperate and respond to their partner's behavior remains unknown (Houston et al. 2005), in large part because it is seldom clear that either parent actually has this knowledge, and because between-sex differences in efficacy of parental duties may shape just how equitable the division of labor is between mates (Parker et al. 2014; Jennions and Fromhage 2017; Yoon et al. 2017). For example, offspring survival usually requires the maintenance of a minimum threshold level of heat for the chemical reactions responsible for growth to occur (Dawson et al. 2005; O'Neal et al. 2008; Nord and Nilsson 2011). However, when offspring require an exogenous source of heat and only one sex – typically females – broods these young, reduced food provisioning by the male and increased begging by nestlings may be costly if it forces females to sacrifice brooding for foraging (either for themselves or for their young). This cost accrues because, in the absence of brooding, nestlings can cool to sub-optimal temperatures, retarding their growth and development (Leonard and Horn 2001; W grzyn 2013; Bowers et al. 2015a; Andreasson et al. 2016; Will et al. 2017). We posit, therefore, that females invariably face a within-individual trade-off between brooding and provisioning, particularly when their offspring are young and have not yet begun to

thermoregulate for themselves, and that selection favors the monitoring of a mate's activity around the nest to inform a female's decision-making and help her establish whether to continue brooding nestlings if he is physically present nearby and likely to deliver food to the brood, or whether she should leave the nest to forage.

We investigated this in a wild population of house wrens (*Troglodytes aedon*, Vieillot), a cavity-nesting songbird. In this species, only the female incubates eggs and broods nestlings for ca. a week posthatching (Johnson 2014) and, when females are brooding nestlings after hatching, they typically receive food at the nest entrance from the male, which they then pass to nestlings (as occurs in a variety of both cavity-nesting and open-nesting species; Johnson et al. 2008; EKB personal observation; see also Nolan 1978; Curlee and Beissinger 1995; Mori et al. 2010; Eckerle and Thompson 2020). Females cannot see outside the nest cavity while brooding; however, brooding females routinely perch at the entrance of the nest and visually inspect their surroundings (Fig. 1), perching and looking out from the nest for a short duration (ca. 10–60 sec) before eventually receding back into the nest cavity or flying away to forage. This behavior was previously documented during incubation and termed a “lookout” (Johnson and Kermott 1991; Ziolkowski et al. 1997), and may also be relevant when rearing nestlings, as looking out from the nest may allow females to determine if their mate is physically present nearby and whether he is likely to deliver food anytime soon. For example, previous research revealed that, when looking out from the nest entrance, females may sing crude songs that act to draw their mate toward the nest if he has been absent for an extended period of time (Johnson and Kermott 1990, 1991; Halkin 1997; see also Langmore et al. 1996), thereby drawing attention to themselves and stimulating provisioning by their mate when food is needed (see also Halkin 1997; Leonard 2008; Boucaud et al. 2016). Thus, females looking out from the nest appear, on some level, to be monitoring the activity or presence of their mate in the immediate vicinity (males do not always sing when provisioning, but usually forage on their territories; Johnson 2014). We posit, therefore, that females looking out from the nest (Fig. 1) while rearing ectothermic nestlings, are, in that moment, in the process of making a decision about whether to remain on the nest and continue brooding or to leave the nest to obtain food. By looking out from the nest, the female can determine whether the male is within sight of the nest and simply choosing not to provision, or whether he is away from the nest, out of her field of vision, where he may or may not be foraging for prey for their nestlings.

Here, we test the hypothesis that females look out from the nest while brooding young to ascertain the presence of their mate nearby. Aside from delivering food *per se*, males also acoustically signal their presence near the nest, and a majority of these vocalizations are coordinated with the delivery of food to the brood of nestlings (Johnson and Kermott 1991; see also Halkin 1997; Leonard 2008; Ladd and Gass 2020; Lowther et al. 2020; Ritchison et al. 2020). Male song can take on a variety of functions, but, when rearing nestlings, a male's singing is usually indicative of his impending delivery of food to the brood, as males in a variety of species frequently sing just before delivering food (Nice and Thomas 1948; Nolan 1978; Johnson and Kermott 1991; Halkin 1997; Leonard et al. 1997; Leonard 2008; Neudorf et al. 2013; Johnson 2014). This singing occurs even while the female is actively on the nest brooding her young (Nolan 1978; Halkin 1997), likely serving as a signal that he is about to deliver food within the next few seconds (Nolan 1978; Johnson and Kermott 1991), possibly

facilitating the efficient transfer of prey from male to brooding female and, given the temporal connection between male singing and provisioning, might condition females' expectation of her mate's arrival (e.g., Balsam and Gallistel 2009). However, males do not always sing when delivering food, even though the female would still benefit from knowing his whereabouts. Thus, we predicted that male singing and food provisioning would shape the frequency with which females visually scanned their surroundings and foraged to find food for their young and themselves. We assessed this by parsing moment-to-moment variation in male behaviors (e.g., the time elapsed from a male's song to his subsequent food delivery and time between successive food deliveries) and relating these to female lookouts and foraging trips. Specifically, we predicted that, if females use male song as a signal that he is nearby and likely to deliver food, she should look out from the nest less frequently when he is actively singing and when singing and provisioning have a close temporal connection. We hypothesize that, when females are looking out from the nest, they are in the process of making a decision about whether to stay and continue brooding or to leave the nest and obtain food; if this is the case, then a female's probability of departing from the nest should vary directly with the timing of her mate's activities. In other words, females should be more likely to stay and continue brooding young if the male has recently sung or delivered food, and they should be more likely to leave to obtain food if the male has been absent or has not sung for an extended period of time. In other words, females should (i) look out from the nest and (ii) leave the nest to forage less frequently when they have information indicating that their mate is nearby and likely to arrive with food.

Although changes in maternal and paternal care may represent a direct response to partner behavior, it is possible that females do not respond directly to their mate but, rather, to the begging of their nestlings (e.g., Leonard and Horn 1996, 1998; Grodzinski and Lotem 2007; Bowers et al. 2019a), without requiring any knowledge of what their partner is doing. Thus, disentangling effects of male behavior from nestling demand requires an experimental approach (e.g., to satiate the brood; see also Hinde 2006). To do this, we experimentally supplemented the diets of nestlings with food shortly after hatching, which significantly reduced their begging intensity (Bowers et al., 2019a). Thus, if looking out from the nest is merely a response to nestling begging, we predicted that females rearing food-supplemented young would look out from the nest less frequently and spend more time brooding their young than females rearing non-supplemented young. We also predicted that, if a female's lookout behavior is related to her expectation of her mate's provisioning activity, then an increased frequency of female lookouts may predict the maintenance of pair bonds or an increasing occurrence of divorce (i.e., instances in which females and males are subsequently present in the breeding population but pairing with different individuals; Kempnaers et al. 1998; Culina et al. 2015a,b). In other words, females might switch mates when their current one fails to meet their expectations. We then tested whether these behaviors had consequences for offspring (e.g., if lookout frequency is more frequent when nestlings are underdeveloped because of reduced provisioning) by quantifying pre-fledging mass, fledging age, and the recruitment of these young as breeding adults in the local population. Finally, we assessed intra- and inter-seasonal costs to adults by analyzing females' probability of producing a subsequent brood later in the season and parents'

probability of returning to breed in future years, predicting that increases in parental effort would reduce the parents' near- or long-term probability of future reproduction.

Methods

Study species and site

House wrens are small (10–12g), insectivorous, secondary cavity-nesting songbirds with a wide breeding distribution. The migratory northern house wren (*aedon* subspecies, *T. aedon aedon*) breeds across the middle section of North America, spanning from the Atlantic to the Pacific Oceans, north of approximately 35° N latitude (biology summarized in Johnson 2014). Females select a mate that is defending a nest site and has built the base of a nest with woody sticks; nest construction is then completed by the female using feathers, grasses, and other soft materials (Finke et al. 1987; Dobbs et al. 2006). Territories, established by males, are usually ca. 0.25–0.5 Ha in size, and males usually remain on their territories when foraging (Johnson 2014). Females in the study population produce a modal clutch size of seven eggs in the first brood of a breeding season and six eggs if a second brood is attempted later in the season (Hodges et al. 2015). As with many species, only the female broods young nestlings, spending ca. half to two-thirds of daylight hours brooding (Johnson 2014; Will et al. 2017), and these females also provision nestlings during this time, gradually ceasing brooding activity and increasing provisioning rate as the brood approaches 8–10 d of age and the nestlings begin to thermoregulate for themselves (Dunn 1976; Bowers et al. 2014b). Males also provision nestlings with arthropod prey after hatching, either directly by entering the nest cavity if the female is absent or by delivering prey to brooding females, which then pass the prey to nestlings early in the nestling stage (i.e., within ca. one week of hatching; Bowers et al. 2014b; see also Brackbill 1970; Curlee and Beissinger 1995; Mori et al. 2010); Nolan (1978) also observed this behavior in the prairie warbler, speculating that the male song served to alert the female of his arrival within the next few seconds. Females may occasionally ingest a proffered prey item themselves, but this is not common. Thus, females have direct knowledge not only of nestling begging intensity but also of paternal food deliveries, at least early in nestling development.

As obligate cavity-nesters, house wrens readily accept nestboxes for nesting. Our study site, with a box-nesting population, is located in secondary deciduous forest in McLean County, Illinois, USA (40.665°N, 88.89°W). Nestboxes have an internal volume of ca. 1700 cm² (height × width × depth = 22 × 8.6 × 9 cm), which is consistent with cavity sizes in other study populations (Lambrechts et al. 2010; Mueller et al. 2019b), and are distributed on a 30-m × 60-m grid, and are placed atop 48.3-cm diameter aluminum predator baffles on 1.5-m metal poles.

Procedures

During the 2014 and 2015 breeding seasons (May–August), we caught adults approximately half-way through incubation using a trap door at the nestbox entrance or a mist net next to the box. We banded both males and females with a unique United States Geological Survey leg band. Males were also banded with three additional colored bands (a total of two bands

per leg), which we arranged in unique combinations to identify each male without having to recapture them.

Once eggs hatched, broods were randomly assigned to one of three food-supplementation treatments (experimental, control, natural/unmanipulated), with new treatments alternated with the successive hatching of clutches. We applied treatments to all nestlings within broods so as to generate a set of truly independent observations (i.e., increased begging of a given nestling often increases the begging of its siblings within broods; Forbes 2002). We also applied another treatment (oral supplementation of corticosterone) as part of another study (Bowers et al. 2019a). However, the effect of this corticosterone treatment on nestling begging was ephemeral and disappeared after only ca. 5 min (Bowers et al. 2019a) and had no overall effect on female lookouts (see Online Resource Table S1); thus, we did not consider this variable further in the current study. Treatments were applied to all nestlings within broods once each day on days 2–5 posthatching (Fig. 1 in Bowers et al. 2019a) by pipetting the supplement into the nestlings' mouths, which they then swallowed. For the food-supplementation treatment (see Table 1 for sample sizes and descriptive statistics), experimental nestlings were fed commercially available baby bird food (Kaytee “exact” Hand-Feeding Formula for baby birds) suspended in water, following the manufacturer's recommendation (on days 2–5 posthatching, nestlings received the following amounts of food suspended in water: day 2: 200 μ L of 10% food; day 3: 300 μ L of 20% food; day 4: 400 μ L of 20% food; day 5: 500 μ L of 20% food). Sham control nestlings were fed the water vehicle only in equivalent volumes as experimental broods of similar age (i.e., the only difference between control and experimental nestlings was their caloric intake, while still activating gut stretch receptors). Both experimental and sham control treatments curtailed begging vocalizations significantly relative to natural, unmanipulated young over the course of our observations (Bowers et al. 2019a).

We quantified nestling begging vocalizations and parental provisioning simultaneously at 4 d posthatching, but occasionally at 5 d if weather precluded an observation of sufficient length the day before. The amount of food delivered to nestlings at this age predicts pre-fledging nestling mass and survival and subsequent recruitment to the breeding population (Bowers et al. 2014b). We recorded nestling begging vocalizations using a small microphone within the nestbox attached to a digital voice recorder (Sony ICD-PX312) outside the box and out of sight from the nest entrance (Barnett et al. 2011; Bowers et al. 2016), and we recorded provisioning to nests and ambient sounds (male songs) using a Kodak Zx1 or Zx5 video camera mounted in a cell-phone holster on a 1.5-m pole ca. 1–2 m from the nestbox. We also recorded these behaviors at 7 d posthatching, but focus here on day 4/5 because this is the age at which nestlings were supplemented prior to our observation (satiety was not manipulated on day 7).

We assessed begging vocalizations per unit time using Raven Pro 1.5 (Cornell Lab of Ornithology), targeting specific features of begging calls (e.g., range of frequencies, duration) to count the number of vocalizations efficiently and accurately in an automated fashion (for further details see Bowers et al. 2016, 2019a). This distinguished different calls even when made at a similar time, and, although imperfect (with occasional false positives or negatives), this approach was able to process large files accurately ($R^2 > 0.97$; see Bowers

et al. 2019a). Males usually sing at or near the nestbox, particularly when delivering prey to the nest (correlation between rates of male singing and food delivery: $r_{143} = 0.405$, $P < 0.001$), so we also tallied the songs sung by males at this time. We could not usually see the male singing in these videos, but it is unlikely that any of these instances were non-focal males as male house wrens are highly territorial around the nest-site (Barnett et al. 2012, 2014; DiSciullo et al. 2019), and the male singing near any nest is almost always the resident male (Halkin 1997; Leonard 2008; Johnson 2014). Poles and a dummy camera were placed 24 h prior to filming to allow parents time to habituate to their presence (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 after parents returned to the nest to resume brooding and provisioning (Bowers et al. 2019b), which provides a sufficiently representative sample of consistent individual differences in behavior, at least in other species in which this has been studied (Schwagmeyer and Mock 1997; Pagani-Núñez and Senar 2013; Lendvai et al. 2015; Murphy et al. 2015). After videos were obtained, we analyzed 60 min of each video starting when a parent first returned to the nest (usually in less than 5 min; Bowers et al. 2019b), tallying parental behaviors (lookouts from the nest, food-provisioning rate, brooding time, and the number of male songs). All behaviors observed in these videos were scored by a single individual (JBJ) who was blind with respect to any treatments. Eleven days after hatching began, we weighed nestlings (± 0.1 g) with electronic balances (Acculab Pocket Pro PP 201) and measured their tarsus length (± 0.1 mm) with dial calipers to obtain measures of nestling condition (Sakaluk et al. 2014). We then monitored nests to determine fledging age, usually 15–17 days posthatching. We subsequently attempted to catch all nesting adults present on the study area in 2015–2018 to identify returning adults and offspring.

Data and analysis

All tests were conducted in SAS (version 9.4), with two-tailed hypotheses ($\alpha = 0.05$). Sample sizes vary among analyses because of missing data (e.g., we could not capture every male). We also centered and standardized input variables to z -scores prior to analysis, such that regression coefficients depict the strength of relationships as a measure of effect size (Schielzeth 2010), with values of 0.1, 0.3, and 0.5 considered small, medium, and large effects, respectively (Rosenthal 1994).

First, we analyzed the temporal association between male singing and food provisioning by comparing the time elapsed between a male's song and his next food delivery against the time from one food delivery to the next and from one song to the next using a mixed-model ANOVA with nest ID as a random effect to account for the non-independence of multiple events occurring within a given observation period. We then analyzed maternal behavior (lookouts from the nest, food-provisioning rate, and time spent brooding during our hour-long observations) in separate, univariate generalized linear mixed models (PROC GLIMMIX) with a Poisson distribution. We analyzed these behaviors in relation to paternal behavior (i.e., time from a male's song to his subsequent food delivery and time from one male food delivery to the next), begging frequency, and brood size as continuous predictors in addition to the nestling-feeding treatment and year as categorical effects. We also included maternal ID as a random effect. Although food supplementation reduced nestling begging vocalizations (Bowers et al. 2019a), effects on maternal behavior are similar to

those obtained when analyzing this model with either the food-supplementation treatment or nestling begging rate (vocalizations per hr) individually (Tables S2, S3 online). We then assessed, each time a female looked out from the nest, the female's probability of leaving the nest to forage in relation to the time since the male last sang and the time since he last delivered food, and we included an interaction between these terms, as we expected the effect of either variable to depend on the level of the other (i.e., females should be more likely to stay if they recently heard a male sing, even if he has not delivered food for some time, and *vice versa*). We also included brood size, year, and nestling begging intensity as fixed effects in addition to maternal ID as a random effect. Females do not respond to any single begging vocalization, but to overall vocalizations per unit time; thus, we assessed nestling begging intensity in real-time "batches" as the total number of begging vocalizations over the 10 min preceding the female's lookout (for females looking out within the first 10 min of our observation, we used the total since the start of the observation).

We then assessed the stability of pair bonds by determining whether females retained their mate in subsequent broods or paired with a different male (i.e., divorced; Kempnaers et al. 1998; Culina et al. 2015a,b). Here, we included only observations in which the female and male were demonstrably present and breeding locally but with different individuals; for example, if a male failed to return to breed, this would not constitute divorce because the female has no choice but to mate with another male. We analyzed these events using a generalized linear mixed model with a binary response and female identity as a random effect, and included maternal behaviors (looking out from the nest, provisioning rate, and time spent brooding), paternal behaviors (frequency of provisioning and singing near the nestbox), and nestling begging frequency as continuous predictors in addition to year as a categorical effect. We also included maternal ID as a random effect. We also assessed effects of parental behavior on offspring pre-fledging mass, fledging age, and recruitment as breeding adults in the local population (most recruits breed at 1 yr of age; Bowers et al. 2014a). We assessed body mass and fledging age using general linear mixed models and recruitment using a generalized linear mixed model with a Poisson distribution to analyze the number of recruits produced. These models included female lookouts per hr in addition to hatching date as a continuous predictor and year as a categorical effect. We also included maternal ID as a random effect.

Finally, we assessed potential costs of parental care by analyzing whether females breeding for the first time within a season bred subsequently that year (i.e., were double-brooded), and whether females or their social mates returned to breed in the population in subsequent years. We assessed these using a generalized linear mixed model with a binary response (double-brooded or not, returned or not), and in each model we included male and female provisioning rates, female lookouts per hr and time spent brooding, and age as continuous independent variables. The probability of being double-brooded is a property of individual females, whereas return rates are relevant to both females and males; thus, we analyzed return rates for both sexes simultaneously. In both models we included individual ID as a random effect.

Results

Female responses to male activity and offspring satiety

The temporal association between a male's song and subsequent food delivery was usually close (i.e., almost 60% of the time, these events occurred within less than a minute of each other; Fig. 2a) and this was tighter and more predictable than that between successive feeding events and between successive songs (i.e., the time from song to song and from food delivery to food delivery was each ca. three times longer than that between song and food delivery, on average; $F_{2, 809} = 241.94$; $P < 0.001$; Fig. 2a inset). With respect to maternal behavior, food supplementation of nestlings primarily affected the trade-off between provisioning and brooding within females (Table 2): when nestlings were supplemented with food prior to our observations, females made fewer provisioning trips and tended to spend more time brooding overall (Table 2). Females also varied in the frequency with which they looked out from the nest (some females never looked out from the nest, whereas others looked out every 4–5 minutes; Table 1), and the frequency with which they did so also tended to vary among food-supplementation treatments, but this effect was weak and there was little actual difference between experimentally fed broods and natural, unmanipulated ones, and the frequency with which they looked out from the nest did not vary with nestling begging intensity (Table 2). This lookout behavior was, however, strongly influenced by the timing of male singing and food provisioning (Table 2), as females looked out from the nest more frequently when a male's food delivery did not immediately follow a song (Fig. 2b). Indeed, the time elapsed between a male song and his subsequent food delivery had the strongest overall effect on female behavior, including the amount of time she spent brooding their young (Table 2); females spent more time brooding their young when there was little temporal separation between a male's song and his subsequent food delivery and when the male provisioned at a high rate overall (i.e., increasing time elapsed from one food delivery to the next is negatively correlated with overall provisioning trips per hr; $r_{92} = -0.353$, $P < 0.001$; Table 2). These patterns are also reflected when analyzing overall rates (behaviors expressed per hr), as the more a male sang near the nest, the less females looked out from the nest to inspect their surroundings, and the more time they spent brooding their young (Table S4 online).

Females looking out of their nest more frequently were overall more likely to leave the nest to provision young ($r_{141} = 0.322$, $P < 0.001$), and there was a strong contribution of male behavior to this, as females were more likely to leave the nest when males failed either to deliver food or to sing for an extended period of time (Table 3; Fig. 3). In fact, there was an interaction between these male behaviors, such that females were more likely to stay on the nest and continue brooding their young if the male had recently sung nearby, even if he had not delivered food for some time, and females were similarly likely to stay and continue brooding if the male had recently delivered food, even if he had not been singing (Fig. 3).

The frequency with which females looked out from the nest was also associated with the maintenance of the pair bond, as females that looked out more during the course of our observations were more likely to divorce, or switch mates, before nesting again (Table 4; Fig. 4a). In addition, there was a marginally non-significant tendency for females that

provisioned more to be less likely to divorce prior to their subsequent nesting attempt (Table 4), but this effect was not significant and driven entirely by a single female who provisioned at an exceptionally high rate (Fig. 4b). If we omit this single datum, the effect of maternal provisioning disappears entirely ($F_{1, 42} = 0.20$, $P = 0.654$), while the effect of lookouts remains ($F_{1, 42} = 6.36$, $P = 0.016$).

Effects on offspring

The frequency with which females looked out from the nest affected neither pre-fledging body mass nor fledging age (Table 5). There was, however, a positive effect of maternal lookouts on the number of offspring recruited as breeding adults within the study population in future years (Table 5).

Costs of parental care

There were no effects of increasing maternal care on the probability that a female would produce multiple broods of young within a given breeding season (Table 6). There was, however, a significant negative effect of overall food-provisioning rate on an individual's probability of returning to breed the following year, an effect that influenced males and females equally (Table 6).

Discussion

Parsing moment-to-moment variation in male and female behaviors revealed a close temporal connection between male singing and provisioning that was also strongly associated with female lookouts. Specifically, females looked out from the nest less often when their mate was actively singing, and when singing and provisioning had a close temporal connection, suggesting that females use male song as a signal that he is nearby and likely to deliver food. These results suggest that females form a temporal map of male behaviors consistent with classical, Pavlovian conditioning (Balsam and Gallistel 2009) in which a male's song provides a conditioned stimulus predictive of his imminent food delivery (unconditioned stimulus). This was further evidenced by the finding that, when females were looking out from the nest, her probability of staying and continuing to brood her young varied directly with signals of a male's immediate presence and provisioning activity. In other words, females looked out from the nest and left to forage less frequently when they knew their mate was nearby and likely to arrive with food, and, because males do not always sing before delivering food, female lookouts may provide a way of checking on tardy males. Indeed, that breeding pairs in which females looked out from the nest more often were more likely to divorce between subsequent broods within breeding seasons further suggests anticipatory effects generated by the male's behavior and that these females were, therefore, monitoring the presence and activity of their mates.

On the other hand, nestling satiety appeared to have little effect on female lookouts, as there was no effect of the food supplementation on whether females looked out from the nest, nor was there any correlation between nestling begging and this behavior (Tables 2, S1–S4). Collectively, these results suggest that females are indeed capable of responding to male behavior independent of nestling satiety. Moreover, we found no effect of offspring begging

on maternal care among the full set of supplemented and non-supplemented nests. Although parents might be selected to respond to begging by increasing food provisioning, they may also be selected not to respond to begging insofar as this might otherwise cause them to provide a greater-than-optimal level of care. Indeed, begging may be a ‘psychological weapon’ (Trivers 1974) that parents must interpret correctly (Godfray 1995; Mock and Parker 1997; Parker et al. 2002; Royle et al. 2002a; Mock et al. 2011; Bowers et al. 2019a).

Depending on the context (e.g., during incubation when males do not deliver food to the nest), some component of looking out from the nest may involve vigilance for predators (Ziolkowski et al. 1997; see also Lima and Dill 1990; Ydenberg 1994; Clinchy et al. 2004; Lima 2009), but several lines of evidence suggest that this is unlikely when rearing nestlings (even if it does happen during other stages of the nesting cycle). For example, females actually produce songs while looking out from the nest, which effectively attracts attention and food from her mate in house wrens and other species (Johnson and Kermott 1991; Halkin 1997; Leonard 2008), suggesting that vigilance has little, if anything, to do with this behavior while rearing nestlings. Moreover, females in the study population actually look out from the nest *less* frequently when the perceived risk of predation is experimentally increased (Dorset et al. 2017), and *more* frequently when their mates provision at a high rate (Table S4). Finally, although a widely accepted explanation for male song after pair formation is that it serves as an “all clear” signal, usually when the female is incubating or is away from the nest (Johnson and Kermott 1991), song when rearing nestlings, in contrast, is principally coordinated with food delivery (Nolan 1978; Johnson and Kermott 1991; Halkin 1997; Leonard et al. 1997). This coordinated singing just before delivering food gradually ceases as nestlings begin to thermoregulate for themselves and females cease brooding (Johnson and Kermott 1991). Thus, singing before delivering food is closely related to female brooding behavior, and we also found that females looked out from the nest more often when their partner was actively provisioning food to their nestlings at a high rate (see Table S4), suggesting that females respond to the coordination of male singing and provisioning, and that a high rate of male provisioning may even shape females’ expectations about his arrival (see also Smith 1980; Bell et al. 2010), consistent with classical conditioning (Balsam and Gallistel 2009). Alternatively, it is possible that female lookouts are reflective of maternal personality or quality (e.g., if poor-quality mothers look out more frequently); however, that a female’s lookout frequency was positively correlated with both her own provisioning rate and the recruitment of her offspring as breeding adults in the local population suggests that lookout frequency is not associated with poor maternal quality.

Although interest in the between-sex coordination of parental care has increased tremendously over recent years, we still lack a comprehensive synthesis of how parents respond to their partner’s behavior. A step in this direction may be provided by the ‘negotiation continuum’ model (Johnstone and Hinde 2006), in which one parent responds to the behavior of the other (McNamara et al. 1999; Schwagmeyer et al. 2002; Hinde 2006; Iserbyt et al. 2019). Depending on the species, parents’ behavior ranges from individuals expressing a fixed level of care regardless of what their mate does (Houston and Davies 1985; Lozano and Lemon 1996; Schwagmeyer et al. 2002) to those that respond positively or negatively to their mate’s level of care (Wright and Cuthill 1989, 1990; Lombardo 1991;

Wright and Dingemanse 1999; Sanz et al. 2000; Smiseth and Moore 2004; Hinde and Kilner 2007; Harrison et al. 2009; Westneat et al. 2011). From these earlier studies, subsequent research has revealed an astonishing degree of coordination between male and female parents (Johnstone and Hinde 2006; Raihani et al. 2010; Johnstone et al. 2014; Marriete and Griffith 2015; Bebbington and Hatchwell 2016; Iserbyt et al. 2017; Leniowski and W grzyn 2018a; Griffith 2019; Johnstone and Savage 2019), but, to our knowledge, no study has yet considered how a mode of care provided by only one sex (i.e., brooding young) might dictate the care provided by their mate. It is important to note, however, that parental negotiation assumes that each caregiver has accurate information about how much care its partner is contributing. This may be observed directly or inferred indirectly through nestling begging and condition (Wright and Dingemanse 1999; Schwagmeyer et al. 2002; Bebbington and Hatchwell 2016), but it is not always clear that either parent actually has this knowledge, and, if so, whether it responds by altering its level of food provisioning accordingly. Nonetheless, our study reveals a mechanism, particularly when ectothermic young require warmth from brooding parents, by which females may obtain this information and respond if their mates fail to contribute their fair share to parental care.

Johnstone and Hinde (2006) theorized that, in a general sense, parents with incomplete information about brood need should tend to match their partner's behavior, and that, when either parent has more information than their mate does, the better-informed parent should work harder and compensate more strongly for changes in their partner's effort. In the context of the current study, brooding females are likely much better-informed about brood need and paternal provisioning, as they spend considerably more time in close contact with begging nestlings, and they also appear to compensate strongly for changes in male provisioning and nestling begging (i.e., when nestlings were experimentally satiated and when males delivered more food, females provisioned less and spent more time brooding). But does reduced provisioning by females really represent compensation if they increase effort in brooding young? What currency does brooding effort contribute to potential negotiations between the sexes?

Although we did not detect any relationship between maternal and paternal food provisioning *per se* in this study, several lines of evidence suggest that different components of parental care do indeed covary between the sexes. First, the strongest effect of the food supplementation treatment was on maternal brooding time, whereby females spent more time brooding when nestlings had received supplemental food and begged less frequently; these females also spent more time brooding their young when males sang at a high rate near the nest cavity, which was strongly associated with his impending food delivery. Consistent with this finding, Will et al. (2017) found that, in the absence of supplemental food, female brooding time was positively correlated with male provisioning, an effect likely mediated by the reduced begging of nestlings when males delivered food at a high rate (see also Fig. 2c). Indeed, in addition to providing food, the incubating of eggs and brooding of young is a critical form of care that enhances nestling growth in house wrens and other species (e.g., Leonard and Horn 2001; Dawson et al. 2005; O'Neal et al. 2008; W grzyn 2013; Bowers et al. 2015a; Mueller et al. 2019).

Although females typically spend ca. half to two-thirds of daylight hours brooding their young (Table 1, Fig. 2c; see also Will et al. 2017), they vary widely in their time spent brooding, and leaving the nest (e.g., to forage if their mate does not arrive with food) not only makes the young more vulnerable to predators, including infanticidal male conspecifics (infanticide occurs at ca. 10–15% of nests; Freed 1986; Johnson 2014), but also can prolong nestling development before nestlings attain a minimum developmental threshold prior to fledging (Carrier and Auriemma 1992; Michaud and Leonard 2000; Bowers et al. 2015a; Mueller et al. 2019). Thus, between-sex coordination of parental care is likely enhanced when females are able to predict the delivery of food by their mate, and may be manifest, not simply by changes in feeding rate, but in other forms of care such as incubating eggs or brooding nestlings (see also Hatchwell et al. 1999; Matysioková et al. 2011; Matysioková and Remeš 2014). For example, 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 multidimensional, yet a large majority of studies investigating parental negotiation center around a single form of care, namely food delivery (but, for exceptions, see Markman et al. 1995; Trnka and Grim 2013). On the other hand, time spent brooding as a form of care is rarely considered (but see also Wolf et al. 1990; Harrison et al. 2009; Parker et al. 2014 for exceptions) but is especially relevant in the context of sexual conflict and the duration of parental care. Indeed, empirical studies of conflict over biparental care have revealed widely variable responses by parents to their partner's effort and often fail to detect any apparent costs of care that may drive said conflict, and we posit that this inconsistency is attributable, at least in part, to difficulty in obtaining consistent measures of compensation and its consequences for offspring. Thus, our understanding of sexual conflict will be incomplete until we consider multidimensional parental care and the division of labor that commonly exists in biparental species (see also Emlen and Oring 1977; Parker et al. 2014; Iserbyt et al. 2017; Savage and Hinde 2019).

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; Iserbyt et al. 2015; Leniowski and W grzyn 2018b). In the context of the current study, the more a male provisions, the more time females can spend brooding their young, and, in a number of species, increases in the temperature of nest microclimates and the amount of time parents spend brooding can positively affect nestling condition (Dawson et al. 2005; Bowers et al. 2015a; Mueller et al. 2019; but see also Salaberria et al. 2014), a trait predictive of subsequent recruitment and lifetime reproduction (Tinbergen and Boerlijst 1990; Young 1996; Both et al. 1999; Bowers et al. 2014a, 2015b). Indeed, we found a close coordination between male singing and provisioning and female brooding, and the frequency of female lookouts increased with male provisioning rate. This latter effect might reflect females' expectations about a male's arrival, but it might suggest, since the number of female lookouts significantly predicted offspring recruitment into the breeding population, that lookouts may also serve as signals to the male to deliver more food (see also Smith 1980; Bell et al. 2010).

Finally, we found that increases in provisioning rate negatively affected the probability that either parent would return 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 the number of young fledged within a year (Greenwood and Harvey 1982; Drilling and Thompson 1988; Hoover 2003), and we controlled for this in our analysis. Effects of provisioning on return rates are often observed in males, but not females (Santos and Nakagawa 2012; Williams and Fowler 2015), and this cost of paternal care for males likely plays a fundamental role in generating sexual conflict, even if males might be the genetic sire of all the young in their nest (Trivers 1972; Parker et al. 2014; Fowler and Williams 2017; Johns et al. 2019). Thus, our results suggest that natural selection acting on male investment in present vs. future offspring may be further shaped by intersexual selection imposed by females.

In conclusion, our data suggest that females look out from the nest, at least in part, to ascertain their mate's presence, and that they use signals (singing and provisioning rate) about their mate's activity to determine whether to stay and continue to brood their young or to leave the nest to forage, with implications for sexual conflict and biparental negotiation. While most research on behavioral compensation has focused directly on the provisioning of food to offspring, comparing maternal vs. paternal provisioning is not likely to provide an accurate representation of the full extent of sexual conflict or responsiveness to partner effort. Parental care is multidimensional, and many species exhibit division of labor between mates, with one sex providing a form of care the other does not. Thus, incorporating multidimensional parental behaviors and division of labor between parents will be necessary to further our understanding of sexual conflict over parental care.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.
A female house wren looking out from her nestbox while perched inside the entrance (photo credit: Dylan M. Poorboy, used with permission)

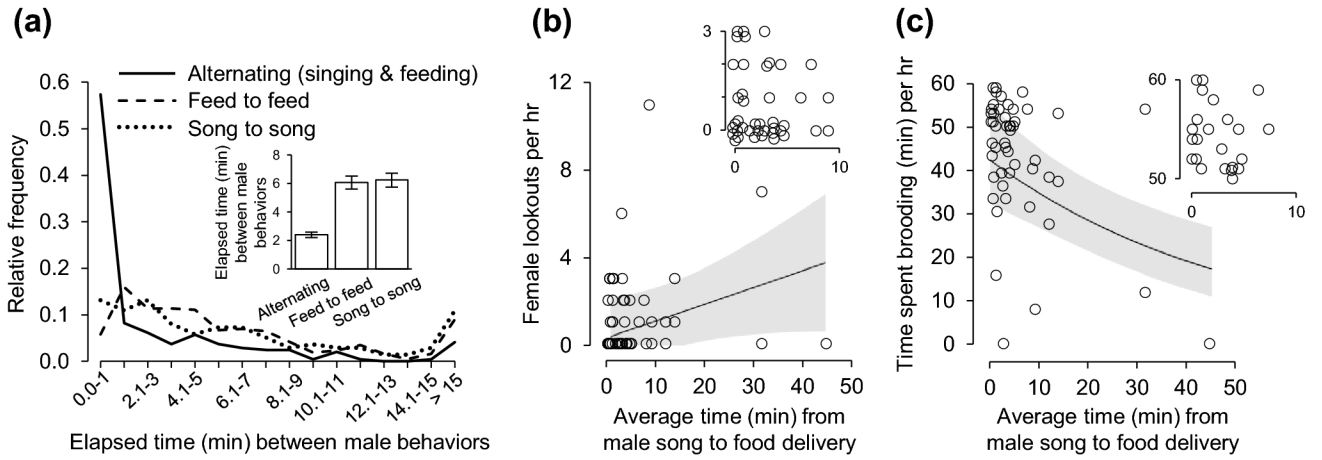


Fig. 2. (a) Relative frequency of latencies (min) between subsequent male behaviors (alternating singing and provisioning, successive provisioning trips, and successive songs), inset is the average time (min) elapsed between these behaviors, (b) frequency with which females looked out from the nest and (c) time spent brooding their young in relation to the time elapsed between a male’s song and his subsequent food delivery. Observations lasted for an hour immediately following nestling supplementation. Means \pm SE are plotted in (a); regression lines in (b,c) depict the fitted predictions \pm 95% CI from a generalized linear mixed model while accounting for the other factors (see Table 2), and inset with each are areas of overlapping data

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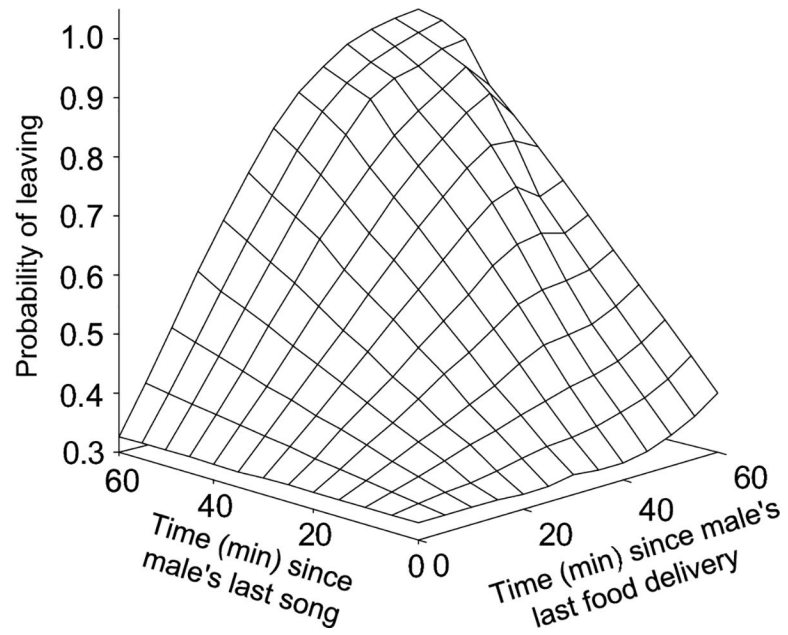


Fig. 3. Probability of leaving the nest in relation to the time elapsed since the male last sang or delivered food. Darker areas indicate an increased probability of leaving to forage and lighter areas a reduced probability, as predicted from a generalized linear mixed model while accounting for the other factors (see Table 3)

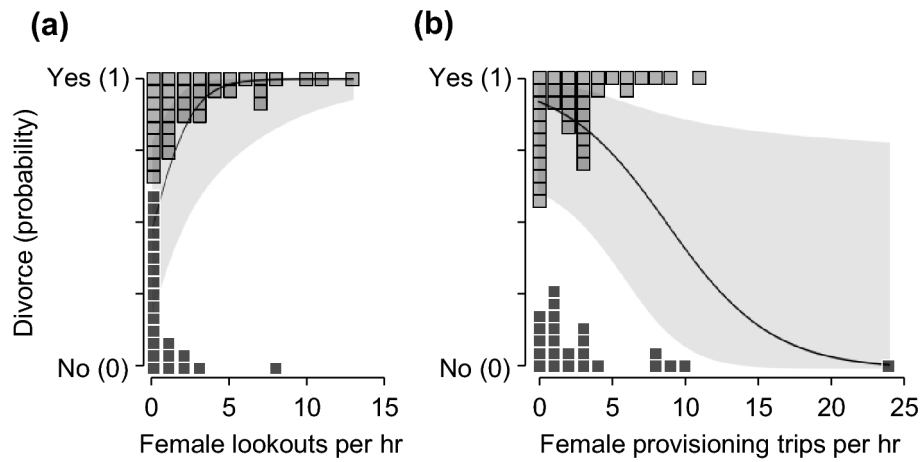


Fig. 4. Probability of divorce, or the switching of mates before a subsequent nesting attempt, in relation to (a) the frequency with which females looked out from their nests and (b) delivered food to the nest during our observations. Regression lines depict the fitted predictions \pm 95% CI from a generalized linear mixed model while accounting for the other factors (see Table 4); light and dark squares are individual observations in which the pair did or did not divorce, respectively

Table 1

Descriptive statistics for nests at which food-supplementation treatments were applied. Experimental nestlings were fed baby bird food suspended in water, control nestlings were fed the water vehicle only, and natural nestlings were handled in a similar way but only had a pipette tip inserted into their mouths

Feeding treatment:	<i>N</i>	# of unique females	# of unique males	Brood size \pm SD
Experimental	53	47	41	5.5 \pm 1.4
Control	50	48	43	5.5 \pm 1.3
Natural	43	41	35	6.0 \pm 1.4
Variables measured:	Mean	Minimum	Maximum	SD
Female lookouts per hr	1.94	0	13	2.78
Female provisioning trips per hr	2.77	0	24	3.33
Female brooding time (min) per hr	41.9	0	60	13.21
Male provisioning trips per hr	3.59	0	23	4.48
Male singing rate per hr	1.24	0	13	2.74
Begging vocalizations per brood per hr	7,064	394	17,762	3,620

Table 2

Maternal behavior (looking out from the nest, feeding, and brooding) in relation to nestling begging and the time elapsed between male activities (time from a given song to the next food delivery and from one food delivery to the next). Times from song to food delivery and between subsequent food deliveries are specific to males. Significant effects in bold type, random effects in italics

	Estimate ± SE	F	df	P
Looking out from the nest:				
Food treatment		3.37	2, 36	0.046
Control ^a	-1.010 ± 0.428			
Experimental ^a	-0.076 ± 0.504			
Time from song to food delivery	0.537 ± 0.188	8.15	1, 36	0.007
Time from food delivery to food delivery	-0.270 ± 0.213	1.60	1, 36	0.214
Nestling begging	0.111 ± 0.187	0.35	1, 36	0.556
Brood size	-0.366 ± 0.248	2.18	1, 36	0.148
Year ^b	1.620 ± 0.628	6.65	1, 36	0.014
Intercept	-0.864 ± 0.580			
<i>Female ID</i>	<i>0.643 ± 0.393</i>			
Food provisioning:				
Food treatment		5.83	2, 36	0.006
Control ^a	-0.908 ± 0.283			
Experimental ^a	-0.836 ± 0.365			
Time from song to food delivery	-0.087 ± 0.128	0.47	1, 36	0.499
Time from food delivery to food delivery	0.095 ± 0.137	0.49	1, 36	0.491
Nestling begging	0.136 ± 0.154	0.78	1, 36	0.383
Brood size	0.108 ± 0.165	0.43	1, 36	0.516
Year ^b	0.139 ± 0.437	0.10	1, 22	0.754
Intercept	0.976 ± 0.377			
<i>Female ID</i>	<i>0.633 ± 0.316</i>			
Time spent brooding:				
Food treatment		4.85	2, 36	0.014
Control ^a	0.249 ± 0.080			
Experimental ^a	0.143 ± 0.093			
Time from song to food delivery	-0.173 ± 0.043	16.00	1, 36	< 0.001
Time from food delivery to food delivery	-0.075 ± 0.033	5.08	1, 36	0.030
Nestling begging	0.043 ± 0.038	1.31	1, 36	0.260
Brood size	-0.060 ± 0.043	1.97	1, 36	0.169
Year ^b	-0.124 ± 0.135	0.85	1, 27	0.366
Intercept	3.665 ± 0.133			
<i>Female ID</i>	<i>0.147 ± 0.076</i>			

^arelative to natural, unmanipulated nestlings;

^b2014 relative to 2015

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Table 3

Probability of female leaving the nest to forage when looking out from the nest entrance. Nestling begging represents total number of vocalizations per brood for a 10-min span before each lookout. Significant effects in bold type, random effects in italics

	Estimate ± SE	F	df	P
Time since male's last song	0.003 ± 0.200	0.00	1, 265	0.989
Time since male's last food delivery	1.313 ± 0.239	30.29	1, 265	< 0.001
Time since song × Time since food delivery	-0.433 ± 0.209	4.31	1, 265	0.039
Nestling begging	0.138 ± 0.220	0.39	1, 218	0.531
Brood size	-0.042 ± 0.191	0.05	1, 177	0.828
Year ^a	-0.613 ± 0.586	1.09	1, 141	0.297
Intercept	0.917 ± 0.553			
<i>Female ID</i>	<i>0.605 ± 0.354</i>			

^a2014 relative to 2015

Table 4

Probability of divorce in relation to nestling begging frequency and parental behavior. Significant effects in bold type, random effects in italics

	Estimate ± SE	F	df	P
Female lookouts per hr	2.216 ± 0.872	6.46	1, 43	0.015
Female provisioning rate	-0.930 ± 0.463	4.03	1, 43	0.051
Female brooding time	-0.467 ± 0.448	1.09	1, 43	0.303
Nestling begging	-0.142 ± 0.418	0.12	1, 32.7	0.737
Male provisioning rate	1.323 ± 0.809	2.68	1, 34.8	0.111
Male singing	-0.119 ± 0.459	0.07	1, 28.8	0.798
Year ^a	-0.753 ± 0.835	0.81	1, 27.9	0.375
Intercept	1.455 ± 0.794			
<i>Female ID</i>	<i>0.638 ± 1.473</i>			

^a2014 relative to 2015

Table 5

Effects of female lookout frequency on fledging age, pre-fledging body mass, and recruitment of nestlings as breeding adults. Significant effects in bold type, random effects in italics

	Estimate ± SE	F	df	P
Pre-fledging body mass:				
Female lookouts per hr	0.051 ± 0.091	0.31	1, 125.6	0.578
Hatching date	-0.145 ± 0.104	1.95	1, 122.8	0.165
Year ^a	-0.379 ± 0.212	3.21	1, 72.0	0.077
Intercept	0.285 ± 0.162			
<i>Female ID</i>	<i>0.016 ± 0.070</i>			
Fledging age:				
Female lookouts per hr	-0.035 ± 0.103	0.11	1, 106.1	0.738
Hatching date	0.078 ± 0.123	0.41	1, 105.5	0.526
Year ^a	-0.298 ± 0.247	1.45	1, 74.0	0.232
Intercept	0.214 ± 0.192			
<i>Female ID</i>	<i>0.033 ± 0.085</i>			
Recruitment:				
Female lookouts per hr	0.238 ± 0.051	21.74	1, 116	< 0.001
Hatching date	-0.245 ± 0.058	17.76	1, 107.4	< 0.001
Year ^a	-0.174 ± 0.126	1.92	1, 104.7	0.169
Intercept	0.401 ± 0.099			
<i>Female ID</i>	<i>0.069 ± 0.035</i>			

^a2014 relative to 2015

Table 6

Effects on future reproduction of females and their social mates. Probability of a second brood is within breeding seasons and returning the following year is analyzed for both members of a breeding pair (provisioning rate is that of the individual subject). Significant effects in bold type, random effects in italics

	Estimate ± SE	F	df	P
Female probability of a second brood:				
Female lookouts per hr	0.240 ± 0.339	0.50	1, 84	0.481
Female provisioning rate	0.168 ± 0.277	0.37	1, 84	0.546
Female brooding time	-0.017 ± 0.313	0.00	1, 84	0.957
Male provisioning rate	-0.043 ± 0.326	0.02	1, 84	0.895
Age	-0.043 ± 0.274	0.02	1, 54	0.877
Number of young fledged	-0.569 ± 0.315	3.27	1, 84	0.074
Hatching date	-3.361 ± 1.203	7.81	1, 84	0.006
Year ^a	1.056 ± 0.612	2.98	1, 37	0.093
Intercept	-1.725 ± 0.896			
<i>Female ID</i>	<i>0.131 ± 0.591</i>			
Probability of returning next year:				
Female lookouts per hr	0.194 ± 0.164	1.40	1, 233	0.239
Female brooding time	0.063 ± 0.152	0.17	1, 233	0.681
Provisioning rate ^b	-0.354 ± 0.167	4.51	1, 233	0.035
Mate's provisioning rate	-0.062 ± 0.161	0.15	1, 233	0.699
Sex ^c	-1.020 ± 0.289	12.47	1, 233	< 0.001
Age	-0.202 ± 0.149	1.82	1, 233	0.178
Number of young fledged	0.300 ± 0.166	3.26	1, 233	0.072
Hatching date	0.034 ± 0.210	0.03	1, 233	0.870
Year ^a	-0.372 ± 0.355	1.10	1, 233	0.296
Intercept	0.228 ± 0.297			
<i>Individual ID</i>	<i>1.035 ± 0.096</i>			

^a2014 relative to 2015;

^bProvisioning rate × sex $F_{1, 232} = 0.27$, $P = 0.606$;

^cfemales relative to males