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ORIGINAL PAPER

Mating opportunities, paternity, and sexual conflict: paternal care in northern and southern temperate house wrens

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Abstract Males are generally predicted to care less for their young when they have more additional mating opportunities, lower paternity, or when their mates care more. We tested these predictions using male provisioning as a proxy for paternal care in two temperate populations of house wrens (*Troglodytes aedon*) with divergent life histories. Males in the migratory, occasionally socially polygynous New York, USA (northern) population provisioned less when more local females were fertile. A similar relationship was only weakly supported in the resident, socially monogamous Buenos Aires Province, Argentina (southern) population, possibly due to the higher density of house wrens there. A relationship between male provisioning and level of paternity within the brood was supported in both populations, but in opposite directions: while males in the southern population provisioned less at broods containing more extra-pair young, males in the northern population provisioned such broods more, contradicting predictions. Males provisioned less when their mates provisioned more in both populations, in agreement with sexual conflict theory. Additionally, the populations both exhibited a positive relationship between male provisioning and nestling age, but differed in the direction of the relationships of male provisioning with date and brood size. Our results suggest that even within a species, life history differences may be accompanied by differences in the determinants of behavior such as paternal care.

Keywords House wren · *Troglodytes aedon* · Parental care · Extra-pair paternity · Sexual conflict

Introduction

Natural selection favors individuals that optimize the balance between the costs and benefits of parental care. The cost of care consists, in part, of lost opportunity for additional matings (Townsend 1986; Magrath and Komdeur 2003), particularly for males, whose reproductive success in most species is more limited by mating opportunities than that of females (Bateman 1948; Wedell et al. 2006). Males are thus predicted to provide less care as their opportunities for additional matings increase. The chief benefit of parental care is reproductive success through the increased

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fitness of the current offspring. This benefit depends on the offsprings' relatedness to the social parent, which can be reduced by extra-pair paternity or brood parasitism (Westneat and Sherman 1993). Males are usually less certain than females of their relatedness to the current offspring (Clutton-Brock 1991; Davies 1992). Since caring for unrelated young likely provides no fitness benefit, males are generally predicted to provide less care as their certainty of paternity decreases (Winkler 1987; Whittingham et al. 1992; Seki et al. 2007). In species with biparental care, the benefits of care are shared by parents, but costs are not. Sexual conflict between parents over parental care then arises because each parent benefits by making the other incur a greater share of the costs of caring (Trivers 1972; Houston et al. 2005; Wedell et al. 2006; Olson et al. 2008).

In brief, current theory predicts that male parental care should be: (1) negatively related to the availability of other mating opportunities (Magrath and Komdeur 2003); (2) positively related to paternity (Winkler 1987; Westneat and Sherman 1993); and (3) negatively related to the female's care, as each individual haggles with its partner (Clutton-Brock 1991; Wedell et al. 2006). These relationships may exist at the species, population, or individual level (Sheldon 2002). Yet our understanding of how males determine levels of parental care is far from complete, as the empirical support for these predictions is highly inconsistent (mating opportunities: Davies 1992; Magrath and Elgar 1997; van Dijk et al. 2010; paternity: reviewed in Alonzo 2010; sexual conflict: Wright and Cuthill 1989, Royle et al. 2002; Schwagmeyer et al. 2002).

The lack of consensus among studies may be related to variation in the life history attributes of their study systems. For example, although no relationship between paternal care and paternity is expected when the level of paternity for individual males is the same across all matings, males are expected to adjust parental care levels according to their paternity in a brood when there is significant variation in paternity across matings of the same male (Westneat and Sherman 1993).

Here, we explore how two populations of house wrens (*Troglodytes aedon*) that differ in life history traits and mating systems also differ in their relationship of paternal care to (1) additional mating opportunities, (2) level of paternity, and (3) the mate's level of care. Since migratory birds have higher mortality and site turnover rates than resident birds, the number of pairs that remain intact across years is expected to be lower in a migratory than in a resident population (Ens et al. 1996). The intensity of sexual conflict is therefore expected to be higher in the migratory northern population than in the resident southern population, since some costs of caring are indirectly shared by individuals that pair with each other repeatedly (Arnqvist and Rowe 2005).

Methods

Study system

During April–August 2003–2007, we studied northern house wrens (*T. aedon aedon*) in patches of mixed deciduous forest at Cornell University Experimental Ponds Units 1 and 2, in Ithaca (42°31 N, 76°28 W), NY, USA (NY). During October–January 2003–2007, we studied southern house wrens (*Troglodytes aedon bonariae*) on a cattle ranch, Los Zorzales, in a study site consisting of three forest fragments each separated by about 50 m of pasture, in General Lavalle (36°26 S, 56°25 W), Buenos Aires Province, Argentina (BA). Both populations bred in nest boxes, which were erected in 2003. Throughout the length of the study, we monitored 225 nesting attempts in NY and 302 nesting attempts in BA. Northern and southern house wrens are generally considered conspecific (American Ornithologists' Union 1998), but are sometimes classified as separate taxa within a superspecies complex (Brumfield and Capparella 1996).

Northern and southern house wrens differ in numerous life history traits. The northern population is migratory, while the southern population is resident year round. The breeding density of house wrens is lower in the northern population than in the southern population (LaBarbera et al. 2010). The northern population has larger clutches (mean: 6.1 vs. 4.9) and shorter nestling and incubation periods than the southern population (Llambías 2009).

Northern and southern house wrens differ in both social and genetic mating system, with social polygyny and extra-pair paternity being more frequent in the northern house wren (Llambías and Fernández 2009; LaBarbera et al. 2010). Male northern house wrens advertise for a second mate, while their first mate incubates. When excess nest sites are available, as is the case in our populations, 25–40% achieve polygyny (Johnson et al. 1993). Male southern house wrens do not advertise for additional mates, and less than 1% are polygynous (Llambías and Fernández 2009). Both social parents generally provision the brood through fledging (at 14–19 days old in the northern house wren; Johnson et al. 2004), although secondary females of socially polygynous males usually receive less or no aid (Johnson et al. 1993). Male removal experiments in northern house wrens suggest that biparental care is usually facultative but can be obligate during harsh conditions (Bart and Tornes 1989). In our populations, males desert their social mates more frequently in the northern population than in the southern population, but the costs of male desertion are similar (Llambías 2009).

Field procedures

We checked inactive nest boxes every 2–3 days, and checked all active nests at least every other day until all nestlings fledged or the nesting attempt failed. We captured adults in mist nets or on the nest using hand nets and marked each bird with a unique combination of colored leg bands and a metal USFW band (in NY) or an aluminum band (in BA). We confirmed social parents through repeated observations of individuals defending nest boxes and provisioning nestlings. Males were considered polygynous if they were observed defending more than one active nest on the same day. The female at the more advanced nest was considered the primary female. We collected blood samples from the brachial vein of adults as well as nestlings aged 8–11 days. Blood samples were stored in lysis buffer for later paternity analysis.

During 2003–2004 in BA and 2004 in NY, we used Hi-8 Sony Handycam video cameras to record parental provisioning. We filmed nest boxes continuously for 4 h beginning 1 h after sunrise using a camouflaged camera placed 5–10 m from the nest box. We filmed nests when nestlings were 1–4, 7–8, and 10–14 days old, which correspond to early (female broods nestlings often), middle (female broods infrequently, nestlings partially feathered), and late (no brooding, nestlings fully feathered) nest stages, respectively. Replicate observation periods at the same nest were spaced at least 4 days apart. From the videotapes, we quantified the number of provisioning trips by each social parent. We defined a provisioning trip as an adult entering the nest box with food in its bill and emerging without the food. We calculated the number of "provisioning trips" as trips per 4-h observation period. Our data do not include information on food load per trip. In both populations, individuals appear to carry only one food item per trip (personal observation), but we did not estimate sizes or caloric values.

We excluded from analyses four northern and three southern nests where adults did not resume provisioning during the first 15 min of recording, as this suggested that the placement of the camera was disturbing the birds. We analysed a total of 119 4-h observation periods at 53 nests in BA (2003: 23 nests, 50 observation periods; 2004: 30 nests, 69 observation periods), and 96 observation periods at 41 nests in NY in 2004. Of the NY observations, 17 were at seven nests where the female was the primary mate of a polygynous male, and 13 were at five nests where the female was the secondary mate of a polygynous male. The social males at all BA nests were monogamous.

Duration of pair bonds

The probability of a male pairing with the same female for multiple breeding seasons depends on both divorce rates and mortality. Using social pairings from 2003 to 2007, we tested whether the proportion of males remaining paired to the same female for more than 1 year differed between the populations.

Fertile females and paternity

We estimated each male's mating opportunities by the number of fertile females within two territories of his territory ("local fertile females") on the date of the provisioning observation. For males observed multiple times, the number of local fertile females was calculated for the date of each provisioning observation. We assumed that females were fertile from 5 days prior to the laying of their first egg until the laying of their penultimate egg (Yezerinac and Weatherhead 1997; Johnson et al. 2002). We focused on local rather than populationwide fertile females because paternity assignments revealed that almost all (90%) of extra-pair sires were no more than one territory away from the territory of the cuckolded male (LaBarbera et al. 2010).

We performed paternity analysis using seven variable microsatellite loci (mean number of alleles per locus: BA, 8.3; NY, 13.1). No locus had a frequency of null alleles > 0.05 or deviated significantly from Hardy–Weinberg equilibrium. We reran analyses to confirm all mismatches with the social father, and chicks with at least one confirmed non-null mismatch with the social father were considered extra pair (see LaBarbera et al. 2010 for detailed paternity analysis procedures). While we were able to calculate the number of fertile females at all nests for which we had provisioning data, we were only able to determine the social male's level of paternity at a subset of these nests: 34 in BA (2003: 20 nests, 2004: 14 nests) and 30 in NY in 2004, of which six were the nests of primary females mated to polygynous males and four were the nests of secondary females. We checked for variation in paternity level between broods with the same social male.

Statistical analysis

All statistical analyses were done in R v. 2.9.2 (R Development Core Team 2009). We used generalized linear mixed-effects models fit by the Laplace approximation (the glmer function from the package lme4; Bates and Maechler 2009) with a Poisson distribution and log link function to examine how the number of male provisioning trips over the 4-h period varied with fixed effects, with the log of the number of nestlings in each brood as an offset. We ran separate models for NY and BA. We first ran models with only the intercept as a fixed effect in order to evaluate hierarchical random effects structures including these factors: nest stage (nestlings 1–4, 7–8, or 10–14 days old), male identity, and nest identity. We used maximum likelihood to determine that the best random effects structure was nest identity alone. We then tested the following fixed effects: Julian date, nestling age, brood size, proportion of extra-pair nestlings, local fertile females, mate's provisioning trips, and the nest status (as the primary nest of a polygynous male, the secondary nest of a polygynous male, or the nest of a monogamous male). The latter was excluded from BA models since all BA males were socially monogamous. We evaluated these models using Akaike's information criterion corrected for small sample size (AIC_C). The model with the lowest AIC_C score is the best supported model, and the Akaike weight for a model is the probability that that model is the best, given the data and the set of models (Akaike 1974; Burnham and Anderson 2002). The relative importance of a variable is the sum of the Akaike weights of the models in which it appears and is interpreted as the probability that that variable is related to the response variable, given the data and the set of models (Burnham and Anderson 2002). We selected confidence sets consisting of models with Akaike weights$\geq 0.1 w_{best}$, where w_{best} is the Akaike weight of the best supported model; this type of confidence set is recommended by Burnham and Anderson (2002). We averaged the confidence set models and calculated relative importance values for each variable using model.avg from the package MuMIn (Barton 2011).

Since males may make binary transitions between provisioning and not provisioning, rather than a continuous adjustment of the level of provisioning (Whittingham et al. 1992), we used Welch two-sample *t*-tests (two-tailed) to compare nests with provisioning males with nests without. We also used Welch two-sample *t*-tests (two-tailed) to compare NY with BA, to compare monogamous with polygynous nests within NY, and to compare the primary and secondary nests of polygynous males.

For visualization, we ran the best supported model of male provisioning as a generalized additive mixed-effects model using the gamm function from the package gamm4 (Wood 2010).

Results

Duration of pair bonds

The populations did not significantly differ in the proportion of males pairing with the same female over multiple breeding seasons (BA: 8/19=42%; NY: 7/23=30%; Fisher's exact test: $P=0.525$).

Fertile females and paternity

The numbers of local fertile females were significantly higher in BA than in NY (BA mean ± SE=2.47±0.15, NY mean ± SE=0.90±0.12, $t_{206}=8.06$, $P<0.001$).

Out of 34, 11 (32%) nests in BA contained at least one extra-pair young, and out of 138, 21 (15%) chicks were extra pair. In NY, these figures were 13 out of 30 (43%) nests and 28 out of 158 (18%) chicks. The proportions of extra-pair young in nests did not differ between the sites (BA mean ± SE= 0.148±0.043, NY mean ± SE=0.177±0.049; $t_{60}=-0.449$, $P=0.655$). Within nests in NY, the nests of monogamous males did not differ from the nests of polygynous males in the proportion of extra-pair young (monogamous mean ± SE= 0.206±0.068, polygynous mean ± SE=0.099±0.047; $t_{28}=1.30$, $P=0.205$), nor did the nests of primary females differ from the nests of secondary females mated to polygynous males (primary females mean ± SE=0.093±0.047, secondary females mean ± SE=0.107±0.107; $t_4=-0.120$, $P=0.910$); however, sample sizes were small and conclusions about the effects of polygyny on extra-pair paternity rates should be made with caution.

At both sites, we found variation in paternity levels among broods with the same social male. Seven out of seven males in NY and five out of six males in BA had different proportions of extra-pair young between broods, with a mean between-brood difference of 0.25 in NY and 0.34 in BA. In both sites, these differences in proportion of extra-pair young equated to a maximum of four offspring. These metrics demonstrate the existence of within-male variation in extra-pair paternity rates, but do not describe it quantitatively. The samples include males who switched females between broods and males who did not, and two of the NY males were polygynous. The within-pair young differences are sensitive to differences in clutch size as well as in extra-pair paternity.

Provisioning

Males provisioned at a higher rate in BA than in NY (mean ± SE provisioning trips per nestling per hour: BA, 2.72±0.15; NY, 1.93±0.15; $t_{209}=3.66$, $P<0.001$), while female provisioning did not differ between the two sites (mean ± SE provisioning trips per nestling per hour: BA, 2.98±0.15; NY, 2.77±0.19; $t_{209}=3.66$, $P=0.379$). Males provisioned less than females at both sites (mean male proportion of the total provisioning: NY, 0.409; BA, 0.465).

Male provisioning rate increased with date; however, in neither population's confidence set did all models include date (Table 1a), and the relative importance of date was <0.50 in both confidence sets (Table 1b). Males provisioned more with increasing nestling age (Table 1a). Nestling age had high relative importance values (Table 1b) and the coefficients of nestling age were relatively large in all averaged models (Table 2). Males in BA provisioned more per nestling for larger brood sizes, while males in NY provisioned larger broods less (Tables 1a, 2). In NY, monogamous males provisioned more than polygynous males, and polygynous males provisioned primary nests more than secondary nests (Table 1a).

Males did not provision during at least one observation period at 10/53 nests in BA and at 8/41 nests in NY, including

1/7 primary nests of polygynous males and 3/5 secondary nests of polygynous males. The number of local fertile females did not differ between nests with and without provisioning males (BA: t_{14}=1.04, P=0.315; NY: t_{26}=1.77, P=0.089). Males provisioned at a lower rate when more local females were fertile in both sites. Local fertile females had higher relative importance values and larger coefficients in models of NY than BA (Tables 1b, 2).

The mean proportion of extra-pair young did not differ between nests with and without provisioning males (BA: t_7= 0.976, P=0.392; NY: t_{31}=−0.794, P=0.437). Males in BA provisioned less at broods with higher proportions of extra-pair young, while males in NY provisioned such broods more (Table 1a). The proportion of extra-pair young in the brood had a high relative importance value in both sites (Table 1b).

Males in both sites provisioned less when their mates provisioned more (Table 1a, Fig. 1).

Discussion

General patterns of provisioning

We explored the determinants of the level of paternal care in a northern temperate and a southern temperate population of house wrens that differ in life history traits. The populations differed in males' responses to date, with males provisioning more at later dates in the southern and less in the northern population; however, date was not well supported as a predictor of provisioning, with low relative importance values and small model-averaged coefficients. The effect of date on provisioning is likely to be complex, as both food availability and the survival probability of the offspring may vary with time (Norris 1993).

Nestling age was among the most supported predictors of provisioning level, and in both sites, males provisioned older nestlings more. Older nestlings likely have higher total energy requirements, as maintenance energy requirements increase with nestling size (Ricklefs and White 1981). Although this may be countered by a reduction in growth energy requirements as nestling growth rates decrease, this effect is likely to be small. Greater provisioning rates with nestling age is consistent with work on several other passerine species (Haggerty 1992; Goodbred and Holmes 1996).

While southern males made more provisioning trips per nestling at larger broods, the opposite pattern was observed in the north. This is consistent with males' greater per-nestling provisioning overall in BA than in NY and may indicate that provisioning in NY is more costly than in BA: for example, males might be less willing to deplete energy reserves when they face long-distance migration in the near future. However, since brood sizes ranged from two to six in BA and from two to eight in NY, the differing results for the two sites do not necessarily indicate different optimal provisioning level curves. If the optimal per-nestling provisioning level decreases at brood sizes above six, for example, because the maximal level of effort is reached or because the nestlings require less energy to maintain homeothermy (Nur 1984), then such apparently different results from the two populations would be expected.

In NY, socially monogamous males provisioned more than socially polygynous males, and polygynous males provisioned primary nests more than secondary nests; however, these results should be taken with caution due to small sample size. Our results agree, in part, with those reported by Johnson et al. (1993), although they found no difference in male provisioning between monogamous and polygynous primary nests. All BA males were socially monogamous.

Table 1 Differences in the models of paternal provisioning for the Buenos Aires (BA) and the New York (NY) populations

(a) The confidence set models

Site	Model	D	NA	BS	FF	EP	MP	MPS	*k* Values	AIC$_C$	ΔAIC$_C$	w_i
BA	1		+	+		-	-	n.a.	6	720.7	0.00	0.48
	2	+	+	+		-	-	n.a.	7	721.7	0.96	0.29
	3		+	+	-	-	-	n.a.	7	723.0	2.34	0.15
	4	+	+	+	-	-	-	n.a.	8	724.2	3.48	0.08
NY	1		+	-	-	+	-	-	9	819.2	0.00	0.68
	2	-	+	-	-	+	-	-	10	821.1	2.66	0.18
	3		+		-	+	-	-	8	823.7	3.92	0.10

(b) The relative importance values

Site	D	NA	BS	FF	EP	MP	MPS
BA	0.38	1.0	1.0	0.23	1.0	1.0	n.a.
NY	0.19	1.0	0.90	1.0	1.0	1.0	1.0

+ Positive coefficient, - Negative coefficient; *blank space* Exclusion, *n.a.* Not applicable (all males in BA were monogamous), *D* date, *NA* nestling age, *BS* brood size, *FF* fertile females, *EP* proportion of extra-pair young, *MP* mate's provisioning, *MPS* nest status (monogamous/polygynous primary/polygynous secondary), *k* number of model parameters, w_i Akaike weight

Table 2 The differences in averaged models of paternal provisioning in the Buenos Aires (BA) and New York (NY) populations

Site	Variable	Coefficient	Std. coefficient	Std. variance
BA	Date	0.00240	0.00117	2.16×10^{-11}
	Nestling age	0.06080	0.00982	6.16×10^{-12}
	Brood size	0.32400	0.01250	5.09×10^{-11}
	Fertile females	−0.00088	−0.00005	8.74×10^{-14}
	Proportion of EP young	−0.25900	−0.00218	4.60×10^{-11}
	Mate's provisioning	−0.01220	−0.01310	1.19×10^{-11}
NY	Date	−0.00010	−0.00006	1.78×10^{-11}
	Nestling age	0.03110	0.00367	5.64×10^{-13}
	Brood size	−0.16900	−0.00695	1.84×10^{-10}
	Fertile females	−0.16500	−0.00620	1.07×10^{-12}
	Proportion of EP young	0.47400	0.00281	3.11×10^{-10}
	Mate's provisioning	−0.01230	−0.01680	2.06×10^{-12}
	Polygynous primary	−0.24500	−0.00300	7.09×10^{-10}
	Polygynous secondary	−4.57000	−0.04760	3.06×10^{-9}

The coefficients are for an exponential model, hence their small magnitude. Values for polygynous primary and polygynous secondary nests are relative to monogamous nests

Std. Standardized, *EP* extra-pair

Fertile females

Males in both sites provisioned less when more local females were fertile, in agreement with model expectations (Houston et al. 2005). However, for the BA population, the coefficient of the number of local fertile females was the smallest coefficient in the averaged model, and two orders of magnitude smaller than the same coefficient in the model for NY.

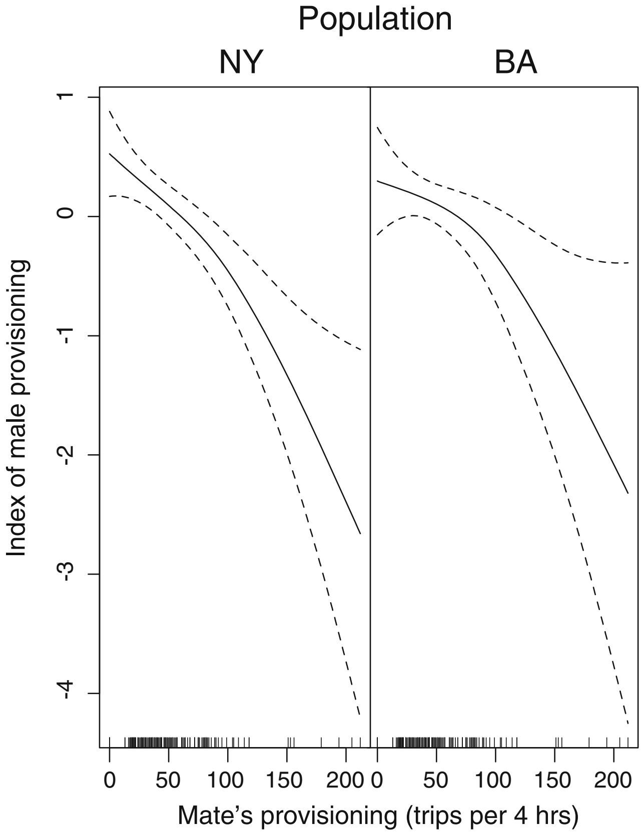

Fig. 1 Male provisioning was negatively related to the social mate's provisioning in both the New York (NY) and Buenos Aires (BA) populations. Vertical tick marks above the *x*-axis indicate data points. - - - 95% Confidence interval

This difference between the populations is not attributable to a lack of local fertile females, since BA had more local fertile females than NY. The higher density, and consequently smaller mean territory size, of birds in BA could contribute to this difference in two ways: (1) the greater physical proximity of local fertile females in BA might enable males to pursue and engage in extra-pair copulations more quickly, and with less cost in lost provisioning time, than in NY; or (2) the smaller territory size might make mate guarding more effective, preventing males from accessing the fertile females and so discouraging them from expending time in this pursuit.

We are unlikely to have missed any larger effect of fertile females on provisioning due to our field methods. Male care during the early morning, when we recorded, is likely to be particularly sensitive to mating opportunities because this is the normal fertilization window for both within-pair and extra-pair copulations in passerines (Birkhead and Møller 1992). For example, fairy martin provisioning rates were more sensitive to other mating opportunities in the early morning (Magrath and Elgar 1997).

Paternity

Although previous work on our populations found higher extra-pair paternity levels in NY (LaBarbera et al. 2010), we found no significant difference in extra-pair paternity rates between the populations. This is likely due to our more moderate sample size, which includes only 1 year for the northern population. We did find within-male variation in both the number and proportion of extra-pair young per brood at both sites, suggesting that it could be advantageous for males to provision less at nests where they have lost substantial paternity.

Despite these similarities, the populations differed in their relationship between male provisioning and level of paternity: while males in BA provisioned less when they achieved lower paternity, males in NY provisioned more, in direct contradiction to models of paternal care and paternity (Winkler 1987; Whittingham et al. 1992; Westneat and Sherman 1993; Kokko 1999; Seki et al. 2007) as well as experimental work on paternal provisioning and paternity in northern house wrens (Brylawski and Whittingham 2004). The relationship between parental provisioning and paternity was strongly supported in both populations, as the proportion of extra-pair young in the brood had relative importance values of 1.0.

That males in the northern population provisioned more at broods in which they had lost more paternity is striking. It may be that this result is not robust, particularly given the moderate sample size for this population. However, the strong statistical support for the paternal provisioning–paternity relationship in this population prohibits an easy dismissal of the result and suggests that it deserves further study.

Sexual conflict

Male provisioning was negatively related to the mate's provisioning in both sites, with relative importance values of 1.0 in both models. The model-averaged coefficients of mate's provisioning did not differ greatly between sites. Since we found no difference between sites in the proportion of pairs that bred together for more than 1 year, this agrees with expectations.

According to Winkler's (1987) model, such an inverse relationship of mates' care is expected when potential offspring production is limited by factors other than parental care. In such cases, it is to the advantage of each parent to minimize its own care as long as its mate will increase care accordingly, resulting in "negotiation" wherein each mate attempts to invest as little as possible without reducing overall reproductive success (Wedell et al. 2006). Such negotiation may occur in real time or, as suggested by Schwagmeyer et al. (2002), provisioning levels may be fixed before the nestlings hatch in the form of a "sealed bid," possibly based on an estimate of the mate's quality. Our results are consistent with those from a study that examined rates of parental provisioning in response to experimental reduction of the partner's care in European starlings (Wright and Cuthill 1989).

Conclusions

Male house wrens in both the northern and southern populations showed a similar adjustment of their provisioning rate in response to nestling age and their mate's provisioning. However, the responses to date, brood size, and extra-pair paternity differed between the populations, and a relationship between male provisioning and additional mating opportunities was strongly supported in the northern population only. These differences illustrate that even within a species, the determinants of behavior, such as paternal care, may vary considerably. Further work on this topic, to determine the specific life history traits underlying this variation, is merited.

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Ethical standards Experiments in this study comply with the current laws of the countries in which they were performed.

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