



Extraterritorial forays and male parental care in hooded warblers

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Extrapair paternity is common among many songbird species yet few studies have quantified male extraterritorial foray (ETF) effort and examined potential trade-offs. One potentially important constraint for males is the need to provide parental care. Current models of male extrapair mating tactics propose that males reduce extraterritorial foray effort later in the breeding season because they face a trade-off between feeding nestlings versus pursuing extrapair matings. However, detailed field studies examining the trade-off between paternal care and male extraterritorial forays are lacking. We used radiotelemetry to quantify male extraterritorial foray effort in hooded warblers, *Wilsonia citrina*, to test the widely held predictions that: (1) males make significantly fewer and shorter forays during the nestling stage relative to other stages (i.e. fertile and incubating stages); and (2) male extraterritorial foray effort is negatively correlated with parental effort. Males made 0.87 ± 0.09 forays/h and spent on average 12.2% of their time foraging off territory. Results were equivocal; some data suggested male foray effort decreased in relation to parental care, while other data suggested otherwise. Pairwise tests controlling for (1) extrapair mating opportunity among males and (2) male, territory and social mate quality revealed a possible trade-off between the mean duration and percentage of time in extraterritorial foray versus providing parental care. Conversely, results also revealed (1) no difference in foray rate, foray duration or percentage of time spent off territory over the various stages of the breeding season, (2) no relationship between male foray effort and male feeding rate, and (3) no difference in foray rate in pairwise comparisons, controlling for variability in extrapair mating opportunity and male quality. Overall, the trade-off between providing male parental care and pursuing alternative mating tactics may not be as strong for male hooded warblers as once hypothesized because males dedicated relatively little time to seeking extrapair copulations off territory.

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During the last decade considerable attention has been focused on the role of territorial intrusions (Westneat 1988; Hanski 1992; Krokene et al. 1996), sperm competition (Briskie 1993; Moller & Briskie 1995; Pitcher & Stutchbury 1998) and extrapair copulations (Morton et al. 1990; Wagner 1992a; Birkhead & Moller 1996) in the evolution of avian mating systems and parental care. In songbirds that are socially monogamous, high percentages of extrapair young within nests can result in males provisioning nestlings that are not genetically related. Recently, there has been a surge of interest in the consequences of male extrapair mating tactics on parental care behaviour in birds (Ketterson & Nolan 1994; Freeman-Gallant 1996; Gowaty 1996a; Magrath & Elgar 1997). Most empirical research has focused on the relationship between certainty of paternity and male parental effort

(see Whittingham et al. 1992, 1993; Wagner 1992b; Dunn & Cockburn 1996; Wagner et al. 1996). A second major focus, that males may face a trade-off between parental effort and extrapair mating effort, has received theoretical but little empirical attention (see Westneat et al. 1990).

The prevailing view of the trade-off between parental care and extrapair mating effort in songbirds is that males significantly reduce extraterritorial foray (ETF) effort later in the breeding season because they face a trade-off between feeding nestlings versus pursuing extrapair matings (Westneat 1988; Westneat et al. 1990; Birkhead & Moller 1992). Feeding rates to nestlings and fledglings can be extremely high (Evans-Ogden & Stutchbury 1996, 1997), and therefore could limit a male's energy available for seeking additional matings outside of the social pair bond. Although this hypothesis is intuitively appealing, field studies that quantify both male foray effort and male parental effort are lacking. Although many DNA fingerprinting studies exist that report the extrapair fertilization frequency for a particular species, few studies

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have quantified male extraterritorial foray effort (see Westneat 1988; Hanski 1992), so few studies have directly tested for these trade-offs. A reason for the lack of data may be that it is very difficult to quantify the frequency and duration of forays by males of many songbird species because of the furtive nature of their extraterritorial forays.

Hooded warblers, *Wilsonia citrina*, provide an excellent opportunity for examining the effects of extraterritorial foray effort on paternal care because (1) extrapair fertilizations are common in hooded warblers (35% of the broods contain extrapair young, Stutchbury et al. 1994, 1997), (2) previous studies have shown that there is substantial variability in both male foray effort (0–0.9 forays/h, Stutchbury 1998) and relative male parental care (25–75% feeding trips to young, Stutchbury et al. 1994) and (3) radiotelemetry is an effective way to monitor extraterritorial foray behaviour in hooded warblers (Neudorf & Pitcher 1997; Neudorf et al. 1997; Stutchbury 1998).

Male extrapair mating tactics can vary from solicitation of extrapair females via song output to actively seeking extrapair copulations on neighbouring territories (Moller 1988; Catchpole & Slater 1995; Stutchbury & Neudorf 1997). In this study we quantitatively examine male extrapair mating effort in terms of extraterritorial foray variables (rate, duration and percentage of time off territory). An extraterritorial foray was defined as an excursion where a male went more than 20 m inside another male's territory (see Neudorf et al. 1997; Stutchbury 1998). Radiotelemetry has revealed that extraterritorial forays are likely for the purposes of seeking extrapair matings because: (1) male hooded warblers intrude onto territories where females are fertile statistically more often than expected by chance and approach fertile females giving conspicuous 'chip' calls 78% of the time (Stutchbury 1998). Because females chip only 20% of the time, males intrude on chipping female territories more often than expected by chance (Stutchbury 1998), (2) 88% (94/107) of the time males do not return to the nest during the first 4 min after a foray, suggesting that they are not foraging for the purposes of gathering food to provision their young (Pitcher 1998), (3) males are rarely (less than 7% (16/256) of the forays) seen foraging off territory (Pitcher 1998) and (4) although actual copulations (within-pair or extrapair) are rarely observed, behavioural observations during telemetry sessions have revealed that males often approach fertile females (within 3 m) during intrusions (Pitcher 1998; Stutchbury 1998). As such, extraterritorial forays are presumably for the purpose of seeking extrapair matings, although other hypotheses are also considered (see Discussion).

In this study, we radio-tracked male hooded warblers during the breeding season when fertilizable females were available, to test whether the amount of parental care provided by a male is negatively correlated with his extraterritorial foray effort. We tested the following specific predictions: (1) males will have fewer and shorter forays during the nestling stage relative to other nesting stages (i.e. prelaying, laying and incubation) due to the burden of parental care duties; (2) males with high extra-

territorial foray effort will have lower food delivery rates than males with low extraterritorial foray effort during the nestling stage; and (3) males with incubating mates will foray significantly more and longer than males with nestlings because incubating female hooded warblers are no longer fertile (Stutchbury et al. 1994; Stutchbury 1998), and other than occasional nest defence, males provide no parental care during this stage.

METHODS

Study Organism and Study Site

Hooded warblers are small, migratory songbirds (11 g) that breed in mixed hardwood deciduous forests. Research was conducted in Crawford County, Pennsylvania (41°N, 79°W) from May to August, 1996 and 1997. The study site is approximately 100 ha in size, supports 40 breeding pairs of hooded warblers, and is gridded with bright orange flagging tape markers every 50 m to allow for easy mapping of locations during radio-tracking sessions (for details regarding the study site see Neudorf et al. 1997; Stutchbury et al. 1994; Stutchbury 1998).

We captured male and female hooded warblers early in the breeding season using playback of male song and mist nets, banded them with U.S. Fish and Wildlife Service bands, and uniquely marked them with coloured plastic leg bands. Standard morphological measures such as wing chord length (mm), weight (g), tarsus, rectrix and plumage score were taken for all adults. We identified and mapped out territory boundaries of all radio-tagged males and adjacent neighbours using male song behaviour (i.e. song posts) and border disputes. We calculated male song output in terms of the percentage of time spent singing for all telemetry sessions.

Radiotelemetry

We mist-netted male hooded warblers, fitted them with radio transmitters using a figure eight harness made from lightweight flexible tubing (see Neudorf & Pitcher 1997) and released them within 5–10 min of capture. We used radio transmitters designed by Holohil Systems Ltd (Woodlawn, Ontario), which are detectable up to 300 m away. Mean radio transmitter weight was 0.67 g (range 0.63–0.85 g), which was on average 5.8% of the body weight of the bird to which they were attached (range 5.4–7.4%). The effect of radio tags on various energetically expensive female and male hooded warbler behaviours has already been examined, revealing no ill effects (see Neudorf & Pitcher 1997; Stutchbury 1998; Pitcher 1998). Stutchbury (1998) and Pitcher (1998) found that tagged males gained as much mass and sang as much as untagged males during the breeding season and tagged males were regularly seen performing complex aerial manoeuvres. Neudorf & Pitcher (1997) also found that female hooded warblers on the same study site fitted with radio tags did not brood or feed nestlings less frequently than untagged females. The findings that energetically demanding activities such as feeding young, singing and

gaining body mass are similar for untagged and tagged males suggests that other aspects of male behaviour are also not adversely affected. We recaptured males to refit them with a new tag as needed (battery life 2–4 weeks). After allowing radio-tagged males 24 h to adjust to the radio transmitter, we located and tracked them with a Lotek STR-1000 or a Wildlife Materials TRX-1000S receiver (Lotek Engineering Inc., Aurora, Ontario; Wildlife Materials Inc., Carbondale, Illinois) and a three-element Yagi antenna.

We tracked 19 males for an average of 14.9 h each (range 6–32 h) during the breeding season (combined total=313 h; nest building and laying: $N=117$ h; incubation: $N=88.5$ h; nestling: $N=107.5$ h). Two males were tracked in both years and we treated each year as independent because each male's mate, territory and neighbours differed the second year. Biologically speaking, these males are likely to be independent, but our results would not differ had we treated them as nonindependent data points.

We defined the fertile stage for females to include both the nest-building and egg-laying stages (Stutchbury 1998). We considered the incubation and nestling stage as the nonfertile period. Total observation time varied among individual males due to variation in radio-tag battery life, poor weather conditions, nest predation, transmitter failure and transmitters falling off prematurely. Transmitters were removed at the end of the breeding season when all telemetry observations were complete.

Male Extraterritorial Foray Effort

To assess male foray effort, we radio-tracked males for 2-h periods at randomly assigned times of the morning (0600–0800, 0800–1000, 1000–1200 hours). We continuously tracked males one at a time using signal strength, male song and visual sightings to monitor male activity at approximately 1-min intervals (see Neudorf et al. 1997; Stutchbury 1998). We recorded the location of the male continuously with the use of a compass and a known grid mark on the study site. During the observation period, we also recorded the occurrence of male and female vocalizations and all intraspecific encounters. While tracking, we stayed 20–30 m from the bird being tracked.

An extraterritorial foray was defined as a foray in which a male travelled more than 20 m inside another male's territory (see Neudorf et al. 1997; Stutchbury 1998). Foray rate was expressed as the number of forays/h and the percentage of time off territory was the proportion of time spent foraging divided by the amount of time that individual was radio-tracked.

Nest Stage and Parental Care

Territories of radio-tagged males and all adjacent neighbouring territories were searched and/or checked every 2–3 days to determine the nest stage of all females. We found nests by following females, by homing in on their conspicuous chips (see Neudorf et al. 1997), or by

Table 1. Extraterritorial foray behaviour of males

Behaviour	$\bar{X} \pm SE$	Range
Intrusion rate (intrusions/h)	0.87 ± 0.09	0.36–2.20
Duration per intrusion (min)	8.57 ± 0.66	5.00–16.50
Total time off territory (%)	12.23 ± 1.4	3.65–25.42

Mean \pm SE values and range calculated from the averages of each male ($N=21$).

Table 2. Extraterritorial foray behaviour of males and duration of individual forays at different times of the day

Time	Foray rate (number/h)	Duration (min)
0600–0800 hours	0.82 ± 0.14 (49)	8.84 ± 0.7 (84)
0800–1000 hours	0.92 ± 0.15 (46)	8.48 ± 0.6 (89)
1000–1200 hours	0.78 ± 0.09 (61)	8.12 ± 0.6 (82)

Sample sizes (number of observation sessions or number of forays) are shown in parentheses.

randomly searching likely nesting habitat. To assess the relative parental contribution of male and female hooded warblers, we set up video cameras to record activity at the nest during the nestling stage. We quantified male feeding rate for an average of 10.1 h per nest (range 6.2–13.9 h) between 1000 and 1400 hours in 1996, and 0600–1200 hours in 1997. Because male parental effort increases with nestling age (Evans-Ogden & Stutchbury 1997), we videotaped parental care when nestlings were 3–7 days old (see Stutchbury et al. 1994). We collected paternal care data for radio-tracked males at five and seven nests in 1996 and 1997, respectively. We quantified paternal care from videotapes by determining the rate of male feeding trips, and in relative terms, the percentage of overall feeding visits performed by the male.

RESULTS

Throughout the 1996 and 1997 breeding seasons we observed 256 extraterritorial forays. A large majority of intrusions (228 of 256, 89%) were to adjacent territories, with the remainder being two territories away. Throughout the entire breeding season, males intruded onto an adjacent territory a mean \pm SE of 0.87 ± 0.08 times/h, with each foray lasting on average 8.6 min (Table 1). Time of day had no significant effect on extraterritorial foray rate (Kruskal–Wallis test: $H_2=0.46$, $P=0.80$; Table 2) or foray duration (Kruskal–Wallis test: $H_2=0.14$, $P=0.93$; Table 2). Therefore, we combined the tracking data from different times of day by individual males for further analyses.

Nest Stage and Foray Effort

We predicted there would be significantly fewer and shorter forays during the nestling stage relative to other breeding stages, due to the burden of paternal care.

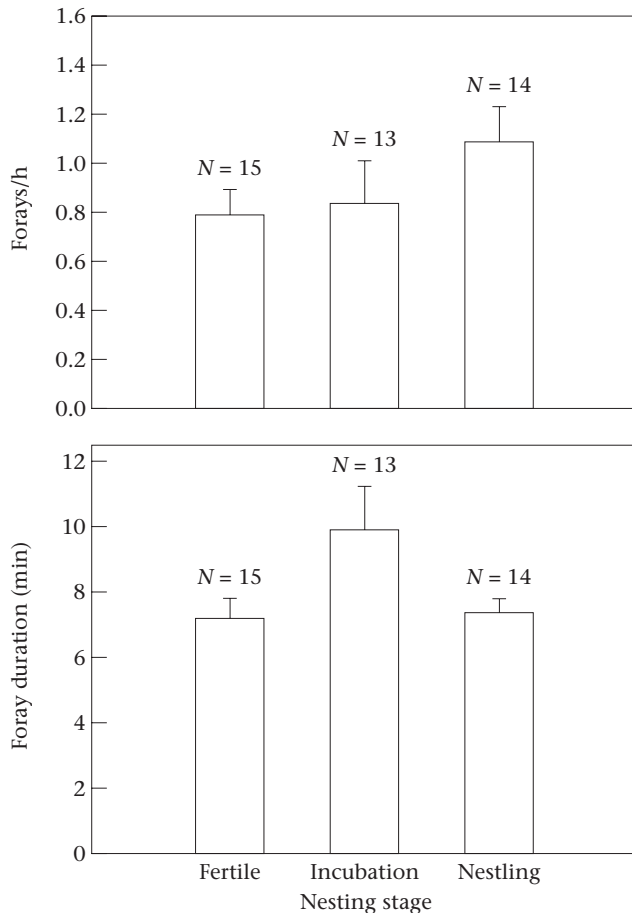


Figure 1. Mean \pm SE foray rate and foray duration versus the nesting stage of the male's mate. Sample sizes (number of males) are given above each bar.

Contrary to this prediction, foray rate did not differ significantly between the fertile, incubating and nestling stages (Kruskal–Wallis test: $H_2=1.71$, $P=0.42$; Fig. 1). Similarly, the average duration of each foray did not vary with nest stage (Kruskal–Wallis test: $H_2=4.66$, $P=0.10$; Fig. 1) and neither did the percentage of time off territory (Kruskal–Wallis test: $H_2=1.10$, $P=0.57$; Fig. 2).

Westneat et al. (1990) suggested that males should pursue extrapair copulations (EPCs) more often early in the breeding season and gradually reduce extraterritorial foray rates later in the season in favour of an increase in paternal care. Contrary to this prediction we found that males did not decrease foray effort later in the 1996 or 1997 breeding season (Kruskal–Wallis test: $H_9=9.00$, $P=0.43$; $H_9=8.89$, $P=0.45$; Fig. 3a, b). Also, males did not foray longer (Kruskal–Wallis test: $H_9=8.94$, $P=0.43$; $H_9=9.00$, $P=0.44$) or spend more time off territory (Kruskal–Wallis test: $H_9=9.00$, $P=0.43$; $H_9=9.01$, $P=0.43$) later in the 1996 or 1997 breeding season.

Paternal Effort and Foray Effort

Feeding rate increases with brood size, therefore both the number of feeds/h and the number of feeds/h per

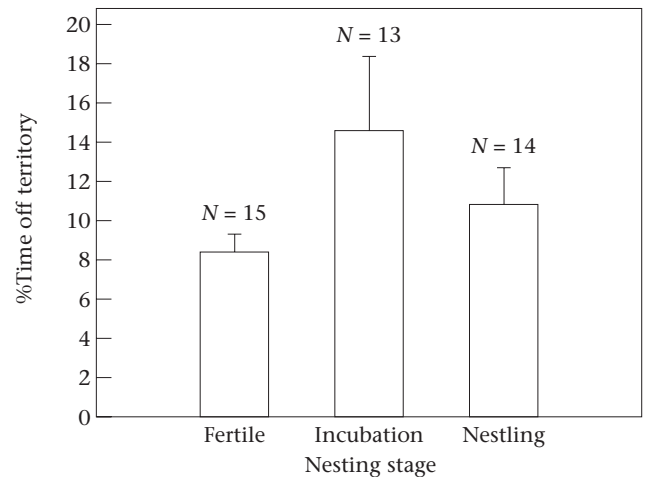


Figure 2. Mean \pm SE percentage of time off territory versus the nesting stage of the male's mate. Sample sizes (number of males) are given above each bar.

nestling were used in all analyses. There was little variation in brood size in the 12 nests examined (range 3–4, $N=2$ and 10, respectively). As in previous studies on the same study site, Evans-Ogden & Stutchbury (1996, 1997) found that time of day had no significant effect on male or female hooded warbler feeding rate between 0600 and 1800 hours. We also found no time of day effect on feeding effort (Kruskal–Wallis test: $H_3=2.83$, $P=0.42$; Table 3) and therefore combined the feeding data from different times of day by individual males for further analyses. The 12 males were videotaped for a total of 121 h (10.1 ± 0.56 h) and the average male feeding rate was 4.63 ± 0.43 feeds/h and 1.21 ± 0.11 feeds/h per nestling.

Contrary to our prediction, males with high foray rates did not feed nestlings at a lower rate (feeds/h: Spearman rank correlation: $r_s=0.15$, $N=12$, $P=0.63$; feeds/h per nestling: $r_s=0.002$, $N=12$, $P=0.99$; Fig. 4), or lower their contribution relative to females (percentage of feeds by male: $r_s=-0.15$, $N=12$, $P=0.61$). There was also no correlation with foray duration; males making longer-lasting forays did not feed nestlings at a lower rate than males making forays of short duration (feeds/h: $r_s=-0.37$, $N=12$, $P=0.22$; feeds/h per nestling: $r_s=-0.39$, $N=12$, $P=0.19$), or lower their contribution relative to females (percentage of feeds by male: $r_s=0.07$, $N=12$, $P=0.82$). The percentage of time spent off territory also did not correlate with feeding rate (feeds/h: $r_s=-0.11$, $N=12$, $P=0.71$; feeds/h per nestling: $r_s=-0.21$, $N=12$, $P=0.47$), or with their contribution relative to females (percentage of feeds by male: $r_s=-0.03$, $N=12$, $P=0.93$).

Male Quality and Extraterritorial Foray Effort

One limitation of using correlation to test for a trade-off between extraterritorial foray effort and parental care effort among individuals is that individual males could vary in quality. High-quality individuals could possibly both feed nestlings and seek extrapair copulations at a high rate and yet still face a trade-off between the two

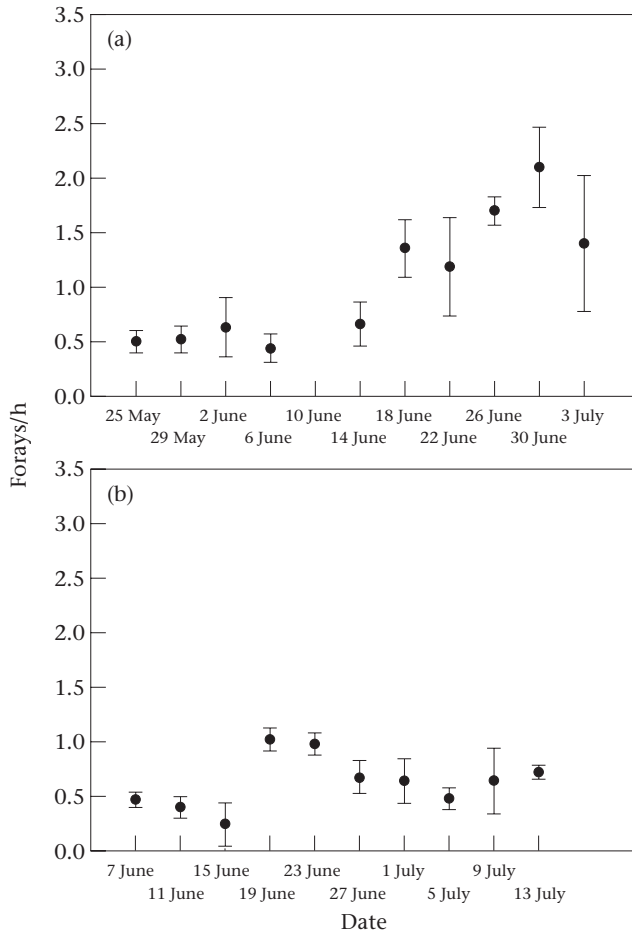


Figure 3. Seasonal variation in average foray rate of males in (a) 1996 (mean first egg date=1 June) and (b) 1997 (mean first egg date=8 June). Data points represent the average over a 4-day period. Sample sizes for foray rate are on average 15.8 ± 2.4 h of observation per point.

Table 3. Feeding behaviour of males at different times of the day

Time	Feeding rate (feeds/h)
0600–0800 hours	4.2 ± 0.45 (24.5)
0800–1000 hours	4.5 ± 0.34 (36.5)
1000–1200 hours	5.3 ± 0.50 (36)
1200–1400 hours	5.2 ± 0.40 (24)

Sample sizes (number of hours of observation) are shown in parentheses.

activities (see Lessells 1991). To determine whether male quality affects intrusion effort during the nestling stage, we examined morphological and behavioural condition-dependent cues for the 12 males for which we gathered paternal care and telemetry data. It is possible that males that are heavier, that sing more, or that are older are of higher quality (Morton et al. 1990; Moller 1988). If there is a positive relationship between extraterritorial foray rate and size, song output or age, this could possibly confound an examination of any potential trade-offs.

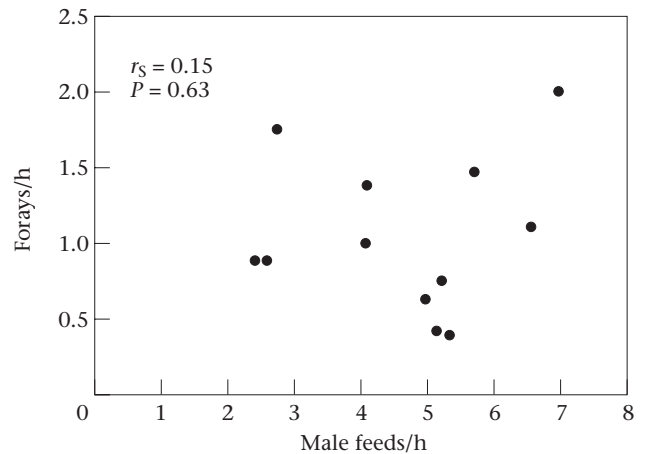


Figure 4. Foray rate versus paternal care (male feeds/h) of radio-tagged males.

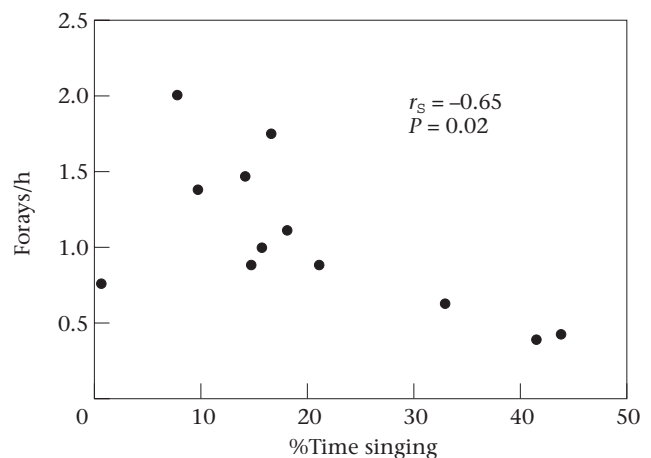


Figure 5. Foray rate versus song output (percentage of time spent singing) of radio-tagged males during the nestling stage.

However, if there was no positive relationship between these measures of male quality and foray effort, then variation in quality would be less of a concern. Only one measure of condition, the percentage of time spent singing, correlated with extraterritorial foray effort, and in the direction opposite to that predicted (percentage of time singing: $r_s = -0.65$, $N=12$, $P=0.02$; mass/tarsus: NS; minimum age: NS; Fig. 5).

Pairwise Comparison of Male Foray Effort

We also conducted two pairwise tests in an attempt to control for variability in male, territory and social mate quality and extrapair mating opportunities for males (i.e. female breeding synchrony).

Extrapair mating opportunities

In this pairwise analysis, we attempted to control for seasonal variability in male extrapair mating opportunities (i.e. female breeding synchrony). Each analysis consisted of a male whose female was incubating and a male that was feeding nestlings. Males were paired on the basis

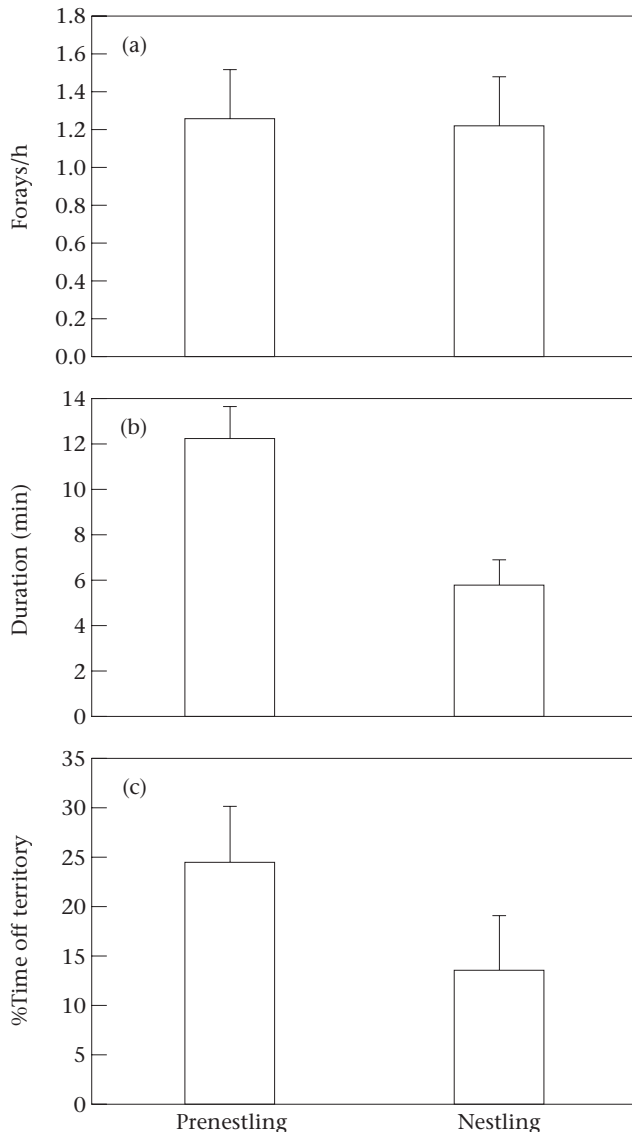


Figure 6. Pairwise comparisons of extraterritorial foray effort variables at nests of males with incubating mates and males feeding nestlings ($N=14$ nests).

of territory proximity (within one territory) and breeding season (i.e. same 5-day period) and thus were faced with similar opportunities for extrapair matings in a spatial and temporal sense. We tracked pairs of males on average 13.2 ± 1.3 h each.

We predicted that males with incubating females would have significantly higher foray rates and longer-lasting forays versus males feeding nestlings. Contrary to prediction, female nesting stage did not affect the rate at which male hooded warblers forayed. We found no significant difference in the foray rate of males whose mates were incubating versus feeding nestlings (Wilcoxon signed-ranks test: $T=0.001$, $N=7$, $P=0.99$; Fig. 6a). However, female nesting stage significantly affected the average duration of forays. Males with incubating females forayed significantly longer on average than did males feeding nestlings (Wilcoxon signed-ranks test: $T=-2.37$,

$N=7$, $P=0.02$; Fig. 6b). Consequently, males with incubating mates had a tendency to spend more time off territory than males feeding nestlings, although this difference was not significant (Wilcoxon signed-ranks test: $T=-1.86$, $N=7$, $P=0.06$; Fig. 6c).

Male and territory quality

By examining the same individual males at different stages of the breeding season, this pairwise analysis attempted to control for variability in male and territory quality and social mate quality and their effects on male foray effort. During the breeding season there were no instances where males remated with a different female and no males switched territories after the study had commenced. Pairs consisted of the same male sampled during different stages of the breeding season: prenestling stage (i.e. without parental care duties) and the nestling stage, at which time males are feeding nestlings. Pairs of males were tracked on average 18.7 ± 1.4 h.

We predicted that males during stages without parental care duties (i.e. prenestling stages) would have significantly higher foray rates and longer-lasting forays versus when they were feeding nestlings. Contrary to prediction, nesting category did not affect the rate at which male hooded warblers forayed. We found no significant difference in the foray rate of males during the prenestling stage and nestling stage (Wilcoxon signed-ranks test: $T=-0.59$, $N=9$, $P=0.55$; Fig. 7a). However, nesting stage tended to affect the average duration of the forays. Males showed a tendency to foray longer on average during the prenestling stage than when feeding nestlings, but the difference was not significant (Wilcoxon signed-ranks test: $T=-2.66$, $N=9$, $P=0.07$; Fig. 7b). Finally, males did not spend more time off territory foraying during the prenestling stage than when feeding nestlings (Wilcoxon signed-ranks test: $T=-0.89$, $N=9$, $P=0.37$; Fig. 7c).

DISCUSSION

Male hooded warblers pursue a mixed reproductive strategy where they contribute substantial parental care and at the same time foray off territory seeking alternative mating opportunities. This study is unique because it attempts to examine quantitatively the trade-off between male parental effort and extraterritorial foray effort using radiotelemetry. Male hooded warblers forayed just as often during the nestling stage as during other stages of the breeding season and males that forayed frequently did not feed their nestlings less often. In contrast to previous observational studies (Westneat 1988; Green et al. 1995; Magrath & Elgar 1997), and a theoretical model (Westneat et al. 1990), these findings suggest that the need to provide parental care does not necessarily constrain males from seeking extrapair copulations. If there were a strong trade-off between extraterritorial foray effort and paternal effort, we would expect a strong negative relationship between measures of these two variables. Contrary to this prediction, we found a positive nonsignificant relationship between male feeding rate and intrusion effort. These results suggest that males

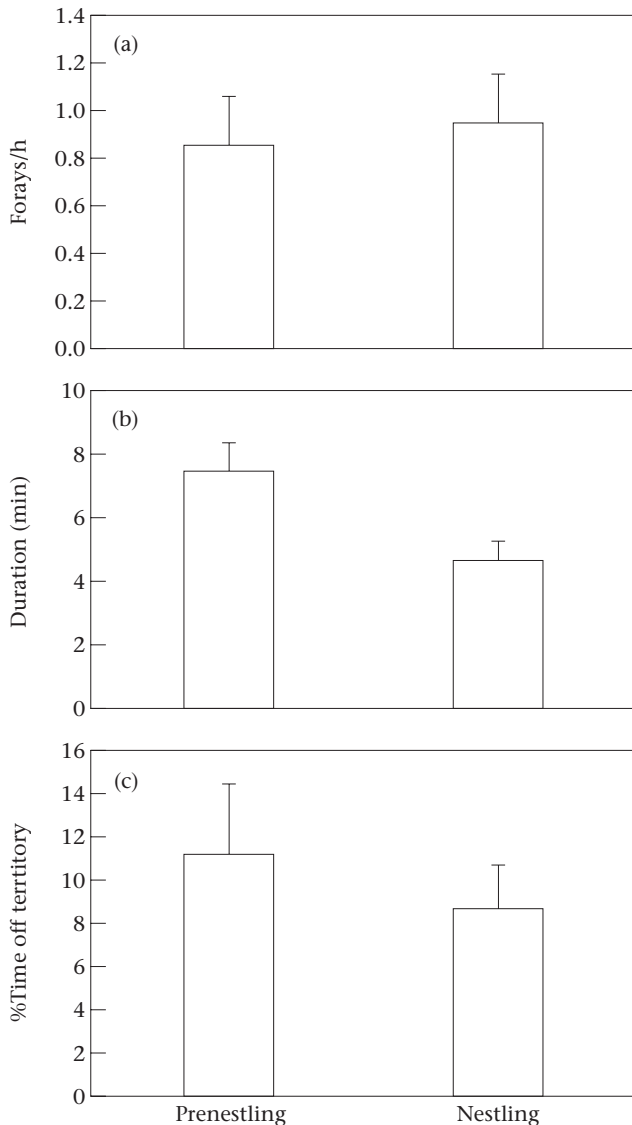


Figure 7. Pairwise comparison of extraterritorial foray effort variables for the same individual males during prenestling (nest building, egg laying and incubation) and nestling stages ($N=9$ males).

performing extraterritorial forays often do not necessarily have lower food delivery rates.

The reason that paternal care probably does not alter male hooded warbler extrapair mating effort may be that males spend relatively little time (12%) outside of their territory foraging. Female hooded warblers make covert forays onto neighbouring territories in order to seek and solicit extrapair matings (Neudorf et al. 1997) and advertise their fertility and location to males via conspicuous chipping (Stutchbury & Neudorf 1997). Stutchbury (1998) found that male hooded warblers preferentially intruded onto territories where females were fertile and approached fertile females giving conspicuous 'chip' calls. Because females chip only 20% of the time, males intrude on chipping female territories more often than expected by chance (Stutchbury 1998). This suggests that the female's advertisement of her fertility and location aid in

making male intrusion effort more efficient. The low percentage of time males spend off territory is probably a consequence of female extrapair mating tactics, rather than males having little or no time available for forays because they are feeding young.

Of all the analyses across breeding stages and seasonal effects, the findings that support the trade-off hypothesis are found primarily in the pairwise test results. These are powerful tests because, despite differences in nest stages of male mates, they control for mating opportunities (i.e. female breeding synchrony), social mate quality and male and territory quality. Both pairwise tests revealed that males forayed as often during the nestling stage as they did during the earlier stages of the breeding season, but there was a significant difference or trend in the duration of forays. Although the sample sizes were relatively small ($N=7$ and 9, respectively), these results suggest that males adjust their extraterritorial mating tactics in terms of foray duration throughout the breeding season. Male extrapair mating effort consists of both foray rate and the duration of each foray, but it is not known how adjustments in either affect the costs and benefits of pursuing extrapair matings.

A correlation between extraterritorial foray effort and parental effort among individuals may be insufficient to detect trade-offs if individual quality affects male foray effort and parental effort (see above). Although no correlations exist in comparisons among individuals, this may occur because high-quality individuals can simultaneously perform extraterritorial forays and feed at a normal rate. Experimental manipulation of male parental effort (via brood size manipulations) would allow one to test whether an increase in male parental effort reduces an individual's extrapair mating effort, regardless of variation in individual quality. In our study, we found that (1) simple measures of male quality were not positively correlated with male intrusion effort, and (2) results of pairwise analyses using the same male, suggest that male quality is not likely to be a confounding variable. An examination of the quantity and quality of food delivered to nestlings by males may also be worthwhile. It is possible that males with high extraterritorial foray rates may compensate by delivering high-quality food less often. Male feeding effort consists of both feeding rate and the quality of food delivered, but it is not known how adjustments in either affect the costs and benefits to males seeking alternative mating opportunities.

Alternative hypotheses for extraterritorial forays

Although evidence is consistent with the notion that forays are for the purposes of seeking extrapair matings, alternative hypotheses are also plausible. One drawback of our study is that we could not always observe male behaviour during the entire radio-tracking session and therefore cannot conclude whether males always participated in extrapair matings or other behaviours during forays. Actual extrapair copulation attempts were rarely observed. Alternative hypotheses for male extraterritorial forays include foraging and expansion of territory boundaries.

Males may foray onto other territories to gather additional food. If males were using forays for foraging purposes, they may be expected to do so during the entire breeding season, early on in the season to gain mass after migration losses and later in the season in order to provision offspring. However, males were observed foraging off territory less than 7% of the time, and 88% of the time males did not return to the nest in the first 4 min after an extraterritorial foray, suggesting that they are not foraging in order to gather food to provision young. Also, few intrusions took place when no female was present (3%, 7/256). To test the foraging hypothesis, territory quality would have to be assessed to compare those males that foraged off territory and those that did not. One would predict that males with low-quality territories (i.e. low food abundance) would forage off territory more often than males with high-quality territories. Because male hooded warblers are territorial and respond aggressively towards other males intruding on their territories, the benefits of foraging on a neighbour's territory would have to be greater than the costs associated with being caught by the resident male (i.e. chasing and fighting, see [Stutchbury 1998](#)).

Males may also intrude onto other territories to expand their territory boundaries ([Birkhead & Moller 1992](#)). However, it is not likely that male hooded warblers attempt to expand their territory boundaries during intrusions because they often move into the centre of the other male's territory and never sing when intruding (see [Pitcher 1998](#); [Stutchbury 1998](#)).

Unlike [Stutchbury \(1998\)](#), we found a significant negative correlation between male song output and foray rate. There is no apparent reason to expect a strong trade-off between singing and extraterritorial intrusion effort because forays are relatively brief. Song output may represent an alternative mating tactic, whereby males elect to sing a lot in the hope of attracting an extrapair mate instead of foraging off territory ([Moller 1988](#); [Catchpole & Slater 1995](#); [Hasselquist et al. 1996](#)). Males may benefit more from singing from their own territory to attract foraging females ([Gowaty 1996b](#); [Neudorf et al. 1997](#)), rather than intruding onto neighbouring territories and risk injury fighting with rival males (see [Stutchbury 1998](#)).

Conclusion

Whether there is a trade-off between extrapair mating effort and male parental care is not a discrete function (i.e. a 'yes' or 'no' question), but rather a continuum ranging from a strong to a weak trade-off between these two behaviours. Evidence for a strong trade-off between extraterritorial foray effort and parental effort in hooded warblers is lacking. Results suggest that for male hooded warblers, which provide parental care only in the form of feeding young, there is no trade-off in the rate at which they foray but rather a trade-off in terms of the duration of time spent on extraterritorial forays in relation to male parental care. In contrast, we predict that in species where males provide substantially more parental care than just provisioning young (i.e. incubating and nest building), they would probably face a stronger trade-off between

parental effort and extrapair mating effort (see [Magrath & Elgar 1997](#)). More observational and experimental studies are needed that examine the amount of time and energy males spend seeking extrapair matings, in order to test more generally the extrapair mating—paternal care trade-off hypothesis.

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