

RESEARCH LETTERS

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Does male extra-territory foray effort affect fertilization success in hooded warblers *Wilsonia citrina*?

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Hooded warbler *Wilsonia citrina* males vary greatly in the frequency and duration of their off-territory forays in search of extra-pair copulations. We used radiotracking and microsatellite parentage analysis in high and low density populations to determine if (1) high foray rate or time off-territory reduces within-pair fertilization success, and (2) if a high foray rate onto the territory of a fertile female increases the likelihood of obtaining EPFs with that female. Males who left their territory often, or for longer periods, did not have lower within-pair fertilization success. Some males repeatedly visited a neighboring fertile female, but in only 3 of 19 cases where radiotagged males visited a fertile female did the male actually sire offspring with that female. Male foray rate onto a fertile female's territory was not a good predictor of whether or not he sired extra-pair offspring with that female. We suggest that mate choice and extra-pair behavior by females may explain why male foray behavior does not correspond closely with actual fertilization success.

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Extra-pair mating systems are typical of most Neotropical migrant passerines, and in many species over 25% of the offspring result from extra-pair fertilizations (EPFs; Griffith et al. 2002, Stutchbury et al. 2005). EPF success varies greatly among individual males creating strong sexual selection in these socially monogamous species (Stutchbury et al. 1997, Webster et al. 2001, Byers et al. 2004). Male extra-pair behavior for many passerines includes frequent intrusions onto neighboring territories to search for fertile females (Westneat 1988, Yezerinac

and Weatherhead 1997, Stutchbury 1998, Woolfenden et al. 2005). Despite the popularity of extra-pair paternity studies, very little is known about the influence of male foray behavior on within-pair and extra-pair fertilization success. In this study we used radiotelemetry and microsatellite paternity analysis to examine how trips off-territory affect male fertilization success in hooded warblers *Wilsonia citrina*, a species with high EPF frequency and frequent off-territory forays (Stutchbury et al. 1997, Stutchbury 1998).

Males who leave their territory for long periods of time in search of extra-pair copulations are expected to have lower within-pair fertilization success if there is a tradeoff between mate guarding and pursuing extra-pair copulations (Dickinson 1997, MacDougall-Shackleton et al. 1996, Currie et al. 1999). Although hooded warblers do not follow their mates closely (Fedy et al. 2002), males do attempt to intercept intruding males and prevent extra-pair copulation attempts on their mate (Stutchbury 1998). Males engaged in frequent or lengthy off-territory forays are presumably less effective in preventing their social mate from accepting copulations from intruding males.

Intrusions onto a neighboring territory are also costly in terms of time, energy, and risk of injury during confrontations with the territory's owner (Stutchbury 1998, Woolfenden et al. 2005). A critical question, then, is how does male foray effort translate into actual extra-pair fertilization success? Males with high foray effort are expected to have a greater chance of achieving EPFs with a given female because repeated intrusions are more likely to overcome the defending male, and/or because a female may judge male quality in part via his persistence and success in intruding on her mate's territory (e.g. Hoi and Hoi-Leitner 1997). High male foray rate to a given fertile female is expected to increase the likelihood that he sires young with that female.

In hooded warblers, male off-territory foray behavior varies greatly between individuals within a population and between high and low density populations (Stutchbury 1998, Norris and Stutchbury 2001). We studied off-territory forays and paternity in two populations of hooded warbler, a high density population in a large mature forest, and a low density population where pairs are distributed among different forest fragments. In high density populations males leave their territory often (0.4 forays/h), average 4.5% of their time off-territory, and visit adjacent territories less than 150 m away (Stutchbury 1998). Males in low density populations also leave their territories often but spend more time off-territory (16.5%) and can travel over 1 km from their territory in search of extra-pair copulations (Norris and Stutchbury 2001). We used this natural variation in male off-territory foray rate and duration to test the predictions that (1) males with a high foray effort during their own mate's fertile period are more likely to suffer paternity losses on their own territory, and (2) males with a high foray rate to the territory of a fertile female are more likely to sire extra-pair young with that female.

Methods

Field site and radiotelemetry

This study was conducted in Crawford County in northwestern Pennsylvania USA (41°N, 79°W) where

hooded warblers are abundant forest birds. Over 95% of males pair monogamously, and territory boundaries are well defined in this species. Male-male chases near females (e.g. extra-pair copulation attempts) are frequently detected during a female's fertile period (Neudorf et al. 1997) although actual copulations are rarely observed due to the dense forest understory. The high density population was located in a 100 ha section of forest that has about 40 breeding pairs annually. In this population males typically have 4–5 close neighbors, and the distance from the edge of one territory to the edge of the next is typically < 30 m. The low density population occupied scattered forest fragments that contained only 1 or 2 breeding pairs per fragment, and the distance to the nearest forest fragment averaged 110 m (range 40–250 m; Norris and Stutchbury 2001). We have described the temporal patterns and variation in male foray behavior in earlier papers (Stutchbury 1998, Pitcher and Stutchbury 2000, Norris and Stutchbury 2001).

In 1996–1997 we radiotracked 11 different males in the high density population from late May to mid June. In 1998–1999, 12 different males were radiotracked in eight small (< 2.5 ha) forest fragments that each contained only 1 or 2 breeding pairs (Norris and Stutchbury 2001). No male was radiotracked in multiple years. Males were fitted with BD-2B (0.67 g) radio-transmitters (Holohil Systems Ltd, Carp, Ontario) using a figure-eight harness (see Stutchbury 1998, Pitcher and Stutchbury 2000, Norris and Stutchbury 2001, 2002 for more details on tagging and tracking). We have found no evidence that the radiotags adversely affect hooded warblers.

Radio-tagged males were observed during 2 h tracking sessions beginning in late May, and continuing for 3–4 weeks. This is the peak period of nesting for this part of the breeding range. Males were followed using a Lotek ST 1000 or Wildlife Materials TRX-1000S receiver with a hand-held three-element antenna. Individual males were observed every 2–3 days, at different times of the morning (06.00–12.00 local time). Territory boundaries were defined by border disputes (counter-singing), regular song locations, and playback of song near boundaries. When males left their territory, we recorded which neighboring territory they visited, the time spent there, and any behavioral interactions with the resident male and female (Stutchbury 1998). We obtained an average of 15.6 h (range: 6–32 h) of observations per male ($n = 23$ males). We defined the "fertile" period of a female as 5 days prior to laying the first egg until the day the penultimate egg was laid which likely corresponds to the period of peak fertility and female receptivity for extra-pair copulations (Neudorf et al. 1997).

We located all nests on the territories of radiotagged males, and where possible obtained small (25–50 μ L) blood samples from both parents and all nestlings (see

Stutchbury et al. 1997 for details). Blood was stored in lysis buffer (Longmire et al. 1992) at 4°C. We also attempted to locate all nests and collect blood samples from families on territories that were visited by radio-tagged males. Predation occurred on about 50% of nests, preventing DNA from being sampled, and we assume predation was random with respect to parentage of the young. Overall, we obtained paternity results for 54 nestlings from 18 broods in the high density population (1996–1997), and for 50 nestlings from 23 broods in the low density population (1998–1999).

Microsatellite methods

We used variation at three microsatellite loci (*Dpu* 01, *Dpu* 03 and *Dpu* 16) previously isolated from yellow warblers *Dendroica petechia* (Dawson et al. 1997) to determine paternity of nestlings (Table 1). To score individual genotypes, we used 50 ng genomic DNA from each individual in a 10 uL PCR reaction that contained 200 uM dNTPs, 0.8 pmol forward and reverse primers, 0.8 pmol fluorescent labelling primers and a standard PCR reaction mix (0.5 U Taq polymerase, 1.5 mM MgCl₂, 0.5M KCl, 0.1M Tris-HCl at pH 8.3, 0.5% TWEEN 20). Following an initial denaturing step of 95°C for 5 minutes, 30 cycles of 30 seconds at 94°C, 30 seconds at 48–50°C (depending on the primer used), and 30 seconds at 72°C were completed. Primers were fluorescently labelled and we attempted to multiplex (i.e. simultaneously load the products of three PCR reactions during the same capillary injection) when possible. PCR products were separated by size (genotyped) using an ABI PRISM 310 Genetic Analyzer (Applied Biosystems). Data were analyzed with the GeneScan® Analysis (version 2.0.2) and Genotyper® (version 2.0) software packages.

All three microsatellite loci were highly variable, with 15 to 28 alleles (Table 1). We calculated the frequency of each allele from the total population of adults genotyped. The expected frequency of heterozygotes did not differ significantly from the observed frequency (chi-square tests, $P > 0.5$), indicating that null alleles were unlikely to be present.

Determination of parentage

Earlier DNA fingerprinting analyses of the same population from 1991–1995 showed that intraspecific brood parasitism was rare (Stutchbury et al. 1997). In this study all nestlings matched the genotype of their social mother. For each nestling we used the remaining microsatellite genotypes to identify which male was the genetic father. We compared all possible father-offspring combinations and any male that could not have contributed that allele was excluded as a possible parent. Thus a mismatch at a single locus resulted in exclusion of the putative genetic father (Jones and Arden 2003). Males were assigned parentage if they matched the nestling at all three loci. There were only two nestlings (from different broods) where more than one male in the population matched the nestling at all loci. In both cases one male was a neighbor, and the other was located ≥ 5 territories away (beyond the range of any foray we documented; Stutchbury 1998) so we assigned parentage to the neighbor.

Overall, 23 of 40 (58%) extra-pair young mismatched their social father at 2 or all 3 loci. For mismatches at a single locus, one should consider whether genotyping errors, null alleles and mutations might account for the mismatch, resulting in a false exclusion (Jones and Arden 2003). Mutation rates are typically low for microsatellites (Jones and Arden 2003), and there was no evidence for null alleles at any of the three loci used (Table 1). When nestlings mismatched their social father at only one locus, their fragment length differed from the social father by an average of 14 bp, suggesting that scoring error can be ruled out and that these nestlings were not false exclusions.

The average probability of paternal exclusion (Table 1) was calculated for each microsatellite locus using CERVUS (version 2.0; Marshall et al. 1998, Slate et al. 2000). This gives the probability that a randomly chosen non-sire male will not possess the paternal allele found in the nestling, given that the mother of the offspring is known (e.g. Jamieson et al. 1994). The total probability of exclusion for all three loci combined was 0.9942.

For some families ($n = 7$) we were unable to obtain DNA samples of females, and for these nestlings whose genetic mother was unknown the combined probability of exclusion for males was 0.9731. We also had some individuals who were only genotyped at two of the three

Table 1. Variability of three microsatellite loci among 78 different adult hooded warblers sampled from 1996–1999, giving the expected and observed heterozygosity, estimated frequency of a null allele, and the probability of exclusion (P_{ej}). The cumulative probability of exclusion was 0.9942 for all loci.

Locus	No. Alleles	Heterozygosity		Freq. null allele (r)	P_{ej}
		Exp (h_e)	Obs (h_o)		
<i>Dpu</i> 01	28	0.956	0.960	0.0058	0.899
<i>Dpu</i> 03	15	0.838	0.852	0.0108	0.666
<i>Dpu</i> 16	19	0.923	0.944	0.0129	0.883

loci. Nestlings were only included in further analyses if the probability of exclusion was ≥ 0.95 .

Statistical analyses

We used multiple logistic regression to determine if foray rate or time off territory increased the likelihood of a male suffering paternity losses in his own nest, which we coded as a binary variable. We also used multiple logistic regression to determine if foray rate onto the territory of a fertile female increased the likelihood of gaining extra-pair paternity (yes, no) with that female. We used SPSS 12.0, and statistical tests were one-tailed unless otherwise noted. For power analysis we used PASS 2005.

Results

EPF frequency

In the high density population (1996–1997), 29/54 (53.7%) nestlings were extra-pair young (EPY) and 12/18 (66.7%) broods contained at least one extra-pair young (EPY). In the low density population (1998–1999), 11/50 (22.0%) nestlings were EPY and 6/23 (26.1%) broods contained EPY.

Our success in assigning paternity to extra-pair young varied among years and sites, reflecting sampling coverage of neighboring males. For the high density population in 1996 we assigned paternity to 11/22 (50%) EPY and had sampled 15/25 (60%) of potential extra-pair sires. In 1997 we identified the extra-pair sire for only 1 of 7 EPY, and in this year sampled fewer males (15/40, 38%). Most extra-pair sires (8 of 9) were from adjacent territories which is consistent with earlier studies (Stutchbury et al. 1997). In the low density population we were able to assign parentage to only 1 of the 11 EPY. In most cases we had sampled at least one male from a nearby fragment, but since males travel up to 1.5 km to visit other territories (Norris and Stutchbury 2001) the percentage of candidate males sampled was likely very low.

Within-pair and extra-pair fertilization success

Extra-pair young occurred in the nests of 6 of 13 radiotagged males, but males who spent longer periods of time off-territory, or left often, were not more likely to lose paternity in their own nest (Fig. 1). We performed a logistic regression analysis using paternity loss as a binary variable (0 = no EPY, 1 = at least one EPY) and foray rate, time off-territory and site (high versus low density) as co-variates. There was no correlation between foray rate and time off-territory (Pearson's correlation, $r = 0.024$, $n = 13$, $P = 0.47$), so

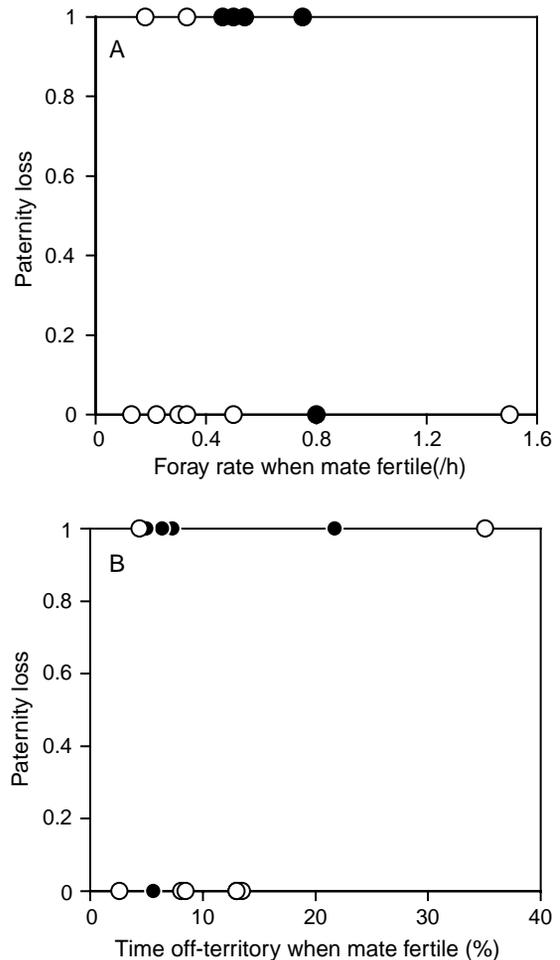


Fig. 1. Paternity loss (0 = no EPY, 1 = at least one EPY) on the territory of each radiotracked male ($n = 13$) versus (A) foray rate and (B) time off-territory when his mate was fertile. High density population (dark circles) and low density population (unfilled circles).

both were included in the model. Foray rate ($t = 1.30$, $df = 1$, $P = 0.255$) and time off-territory ($t = 1.87$, $df = 1$, $P = 0.172$) did not have a significant effect on whether a male lost paternity, and neither did site ($t = 1.54$, $df = 1$, $P = 0.215$). This logistic regression has a power of 0.80 at 0.05 significance level (1-tailed) to detect a change in the probability of losing paternity from the mean value of the dependent variable (0.50, since overall 50% of males lost paternity irrespective of foray behavior) to 0.80, when the value of the dependent variable is increased to 1 SD above the mean. In other words, we have reasonable power to detect if males with a high foray rate (1 SD above the mean) have an 80% chance of losing paternity in their own nests, rather than the background level of 50%.

Almost all radiotracked males made forays onto neighboring territories when the female there was fertile (Fig. 2), yet most sired no extra-pair young on the territories that they visited. For each male we determined

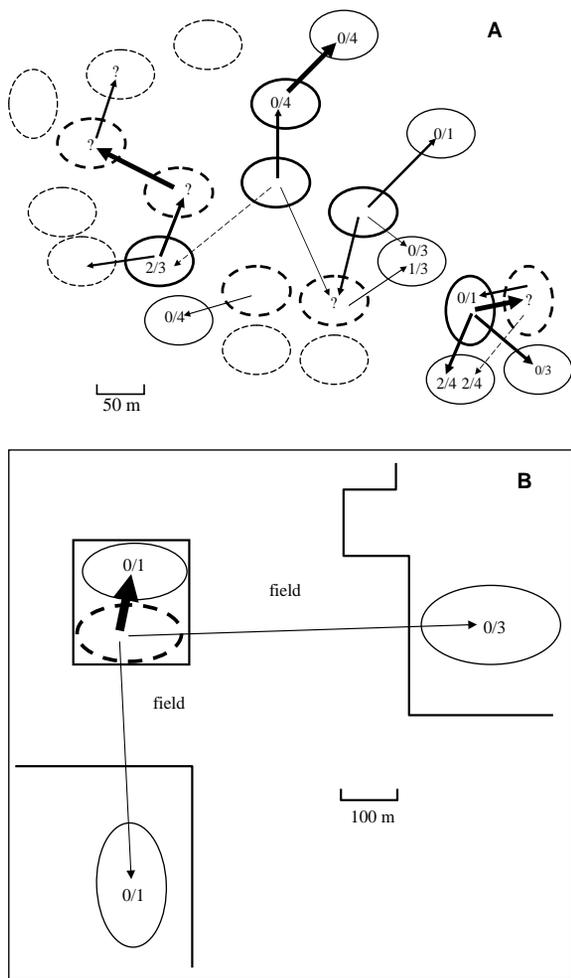


Fig. 2. Diagram showing the territories of radiotracked males (bold) and other males in (A) the high density site in 1996 and (B) a representative forest fragment in 1999. The arrows indicate the territories upon which radiotracked males intruded when the female there was fertile. The width of the arrow indicates the foray rate to that territory by increasing increments of 0.1 intrusions/h (≤ 0.1 , ≤ 0.2 , ≤ 0.3 , ≤ 0.4 , ≤ 0.5 , ≥ 0.5). Solid boundaries indicate we obtained paternity results from the fertile female's nest on that territory, dashed boundaries are territories where nests were preyed upon. At the end of each foray arrow, we indicate how many offspring that extra-pair male sired out of the total brood sampled. In two cases (dashed arrows) males sired extra-pair young on territories they were not known to visit.

the number of hours we had tracked him while a particular neighbor was fertile (range 4–12 h), and the number of trips he made to that territory (range 0–7 trips). Some males repeatedly visited the same neighboring female, but rarely (or never) visited other females an equivalent distance away. We examined whether high foray rate onto the territory of a fertile female increased the likelihood of obtaining extra-pair young with that female. For this analysis each neighboring territory (e.g. potential extra-pair female) was considered a data point because we assume that neigh-

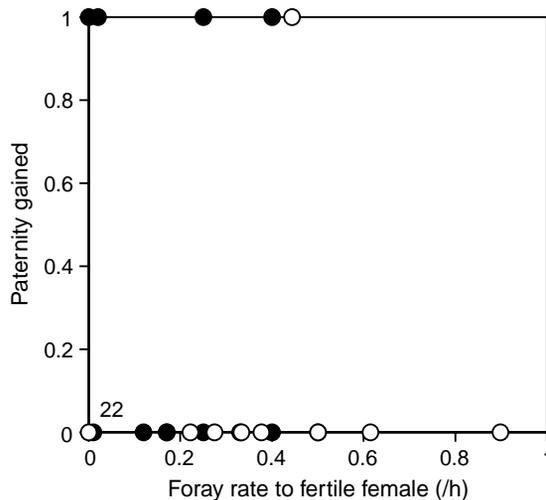


Fig. 3. Paternity gained (0 = no EPY, 1 = at least one EPY) with a female versus foray rate per hour onto the female's territory when she was fertile ($n = 44$ male-female combinations). There were 22 data points for males in the high density population making no forays to an adjacent territory and siring no young there. High density population (dark circles) and low density population (unfilled circles).

boring females independently produce extra-pair young and male foray behavior also varies from neighbor to neighbor. In only 3 of 19 (15.8%) cases did males actually sire extra-pair young (EPY) on territories where we know they visited the female when she was fertile (Fig. 3). Two other males sired EPY with neighboring females that they did not visit during our radiotracking observations (Figs. 2 and 3). Logistic regression analysis showed that foray rate ($t = 0.45$, $df = 1$, $P = 0.50$) and site (high versus low density) did not have a significant effect ($t = 1.07$, $df = 1$, $P = 0.30$) on the likelihood of gaining at least one EPY with a given fertile female. This logistic regression has a power of 0.90 at 0.05 significance level (1-tailed) to detect a change in the probability of gaining paternity from 0.10 (overall 10% of males gained extra-pair paternity) to 0.34 when the value of the dependent variable is increased to 1 SD above the mean. In other words, we have high power to if males with a high foray rate have a 34% chance of gaining paternity with that female compared with a likelihood of only 10%.

Discussion

This is one of the first studies to examine the effect of male foray behavior on fertilization success. Male hooded warblers have a high foray effort (0.4 trips/h, 4–6 min/foray) both during and after the fertile stage of their mate (Stutchbury 1998). Male foray rate and time off-territory when his mate was fertile were not related to whether or not the male lost paternity on his territory (Fig. 1). Our modest sample size did not allow us to test

whether male age or size influences this relationship. For instance, it is possible that smaller or younger males are at a disadvantage in male-male competition for fertilizations (Kempnaers et al. 1995, Wagner et al. 1996) and these males could face a tradeoff between seeking extra-pair matings versus preventing intruding males from approaching their mate.

Male hooded warblers direct most of their forays (84%) toward females that are fertile (Stutchbury 1998), yet despite the high foray effort by some males, most males sired no extra-pair young on territories where they visited a fertile female (Figs. 2 and 3). Males who make frequent forays do not necessarily sire more extra-pair young as a result. We conducted our radiotracking observations from 0600–1200, and although there is no significant variation in male foray effort within this time frame (Stutchbury 1998) it is nevertheless possible that male forays at other times of day (e.g. dawn) are more effective in terms of gaining paternity. In yellow warblers, males that were captured off-territory during systematic netting were not more likely to sire EPY compared with males that were never caught off-territory (Yezerinac and Weatherhead 1997). In many species females exercise a great deal of physical control over which male copulates with them, and females are selective in which intruders they copulate with (Lifjeld and Robertson 1992, Dickinson 1997, Currie et al. 1999). High quality males may face little risk of cuckoldry if their social mate can reject unwanted copulations (Kempnaers et al. 1992, Wagner et al. 1996) and high quality males may obtain EPFs with neighboring females even their own foray effort is low. Many studies have found that male physical and vocal traits correlate well with extra-pair fertilization success (Hill et al. 1994, Hasselquist et al. 1995, Greene et al. 2000, Otter et al. 2001, Thusius et al. 2001), so it is possible that the attributes of male hooded warblers (e.g. song, coloration) are more important in determining fertilization success than their foray behavior.

Two radiotracked males sired young on territories they were not known to visit (Fig. 2). One possibility, of course, is that they visited those territories outside of our observation periods. Another possibility is that they never did visit those territories but that female visited the male during a female off-territory foray (Neudorf et al. 1997). In superb fairy-wrens *Malurus cyaneus*, for instance, females make forays to neighboring territories and all extra-pair young produced by radiotracked females were sired by a male visited during their forays (Double and Cockburn 2000). In hooded warblers most females make forays to neighboring territories and visit multiple males, though extra-pair young are not necessarily sired by males that the female was observed visiting (Neudorf et al. 1997). If females make off-territory forays for extra-pair copulations, then

male forays for extra-pair copulations may not be a strong determinant of male fertilization success.

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