



OFF-TERRITORY FORAYS AND GENETIC MATING SYSTEM OF THE WOOD THRUSH (*HYLOCICHLA MUSTELINA*)

MELISSA L. EVANS,¹ BRIDGET J. M. STUTCHBURY, AND BONNIE E. WOOLFENDEN

Department of Biology, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada

ABSTRACT.—Extrapair fertilizations (EPFs) are an important component of many socially monogamous mating systems. However, information about the reproductive tactics used by male and female birds in extrapair mating systems is still rare. We used radiotelemetry to measure territory use, forays, and mate association in Wood Thrush (*Hylocichla mustelina*) when females were fertile and not fertile. We also conducted paternity analysis to determine the frequency of EPFs in our study population. Socially paired male and female Wood Thrush maintained a close physical association while on their own territory. Most of the off-territory forays observed during the fertile stage were conducted by social pairs. Lone males rarely engaged in off-territory forays during their mate's fertile period but made relatively frequent off-territory forays when their mates were not fertile. Male Wood Thrush may trade-off investment into paternity assurance and extrapair tactics by favoring a mate-guarding tactic when their within-pair paternity is most at risk. The overall rate of EPF (6%) exhibited by Wood Thrush is low compared with other synchronously breeding avian species. We suggest that extensive on- and off-territory mate association throughout the females' fertile period may limit female extrapair mating opportunities and also limit a male's ability to interact with any soliciting extrapair females. *Received 14 August 2006, accepted 2 March 2007.*

Key words: extrapair mating, *Hylocichla mustelina*, off-territory forays, paternity, radiotelemetry, Wood Thrush.

Excursiones Hacia Afuera del Territorio y Sistema Genético de Apareamiento de *Hylocichla mustelina*

RESUMEN.—Las fertilizaciones sucedidas por fuera de la pareja (fertilizaciones extra-pareja) son un componente importante de muchos sistemas de apareamiento socialmente monógamos. Sin embargo, la información acerca de las tácticas reproductivas empleadas por los machos y las hembras en los sistemas de apareamiento extra-pareja es todavía escasa para las aves. Utilizamos radiotelegrafía para medir el uso de los territorios, el abandono de éstos y las asociaciones de pareja en *Hylocichla mustelina* durante períodos en los que las hembras estaban fértiles y en períodos en los que estaban infértiles. También realizamos análisis de paternidad para determinar la frecuencia de las fertilizaciones extrapareja en nuestra población de estudio. Los machos rara vez abandonaron sus territorios sin sus parejas durante el período en que éstas estaban fértiles, pero lo hicieron con relativa frecuencia mientras sus parejas no estaban fértiles. La mayoría de las excursiones hacia afuera del territorio observadas durante el período fértil fueron realizadas por las parejas sociales. Los machos rara vez forrajearon solos por fuera de sus territorios durante el período en que sus parejas estaban fértiles, pero los abandonaron con relativa frecuencia mientras sus parejas no lo estaban. Los machos podrían presentar una selección de compromiso entre asegurar su paternidad e involucrarse en tácticas extra-pareja, favoreciendo una táctica de cuidado de su pareja durante los momentos en que su paternidad está más en riesgo. La tasa total de fertilizaciones extra-pareja exhibida por *H. mustelina* (6%) es baja en comparación con la de otras especies de aves que presentan reproducción sincrónica. Sugerimos que la asociación estrecha de los machos con sus parejas durante el período fértil tanto dentro como fuera de sus territorios podría limitar las oportunidades que tendrían las hembras para tener apareamientos extra-pareja, así como la habilidad de los machos para interactuar con hembras extra-pareja.

MALE BIRDS MAY engage in a mixed reproductive strategy by socially pairing with one female and seeking promiscuous copulations with females outside the social pair (i.e., extrapair) to increase their overall reproductive success (Trivers 1972). Females may also pursue or engage in extrapair matings for both indirect (good genes) or direct benefits (Jennions and Petrie 2000, Foerster

et al. 2003; but see Westneat and Stewart 2003, Arnqvist and Kirkpatrick 2005). These important fitness consequences have resulted in an enormous body of research on the genetic mating systems of socially monogamous birds; at present, the extrapair mating systems of > 130 species of birds have been studied (Griffith et al. 2002, Stutchbury et al. 2005). However, only a handful of

¹Present address: Department of Biology, University of Western Ontario, 1151 Richmond Street, London, Ontario N6A 4B8, Canada. E-mail: mevans28@uwo.ca

studies have investigated the behavioral mechanisms that control rates of extrapair mating in a species, and little is known about sex differences in foray behaviors within or between species. In Hooded Warblers (*Wilsonia citrina*) and Common Yellowthroats (*Geothlypis trichas*), males and females make independent forays, primarily to adjacent territories (Neudorf et al. 1997, Stutchbury 1998a, Fedy et al. 2002, Pedersen et al. 2006). In Acadian Flycatchers (*Empidonax virescens*), only males appear to make off-territory forays, but these are to distant territories (Woolfenden et al. 2005, B. J. M. Stutchbury unpubl. data); in the Superb Fairy-wren (*Malurus cyaneus*), females make off-territory forays that result in extrapair fertilizations (EPFs; Double and Cockburn 2000).

These studies have demonstrated that both males and females may actively pursue extrapair copulations (EPCs). When females engage in copulations outside the social pair, it is expected that males would evolve reproductive counter-tactics that limit paternity losses (Parker 1979). It is possible that male investment into a mate-guarding tactic may also play a role in explaining the rate and pattern of EPF that is expressed by a species. During the breeding season, passerine males have been shown to guard their social mates while on their own territory (Birkhead and Møller 1992, Birkhead 1998, Burley and Parker 1998), but it has been suggested that off-territory forays enable females to avoid male paternity-assurance tactics (Gowaty 1994). Effective mate guarding should require that males stay close to their fertile social mates both on and off territory (Johnsen et al. 1998, Stutchbury and Neudorf 1998). However, the extent to which males can assure paternity with their foraging social mates has never been documented.

In addition to behavioral tactics, factors such as breeding synchrony of a population may influence the extrapair mating opportunities for both males and females. In synchronously breeding populations of birds, such as are found in temperate ecosystems, most females are fertile at the same time. As a result, male birds are faced with the need to simultaneously invest in extrapair and within-pair reproductive tactics and will face behavioral trade-offs that maximize reproductive opportunities (Grafen 1980, Birkhead and Biggins 1987, Westneat et al. 1990). In synchronously breeding birds, male behavioral trade-offs and female control over copulation opportunities are likely to have an important influence on rates of EPF exhibited by a species. Estimates of male and female behavioral investment into extrapair and within-pair (e.g., male mate-guarding) activity in synchronous mating systems have been extremely difficult to obtain (Stutchbury 1998a), but these estimates are necessary to determine how each sex influences the rate of EPFs.

We used radiotelemetry to investigate investment into the reproductive tactics of male and female Wood Thrush over two breeding seasons. We quantified the effort and timing allocated to off-territory activity in Wood Thrush social pairs and determined the physical proximity maintained between socially paired males and females both on and off territory. To assess the outcome of within-pair and extrapair interactions, we conducted parentage analysis using microsatellite genotyping. We hypothesized that high levels of off-territory activity of females would correspond to female peak fertility. Male off-territory forays were expected to occur most frequently outside their social mate's fertile stage, because males in synchronously breeding populations cannot simultaneously maximize their within-pair and extrapair mating

opportunities. Previous research on this species provided anecdotal evidence for extrapair interaction and male mate-guarding (Roth et al. 1996). However, the extrapair mating system of the Wood Thrush has not previously been studied.

METHODS

The Wood Thrush is a socially monogamous, Neotropical migratory songbird, inhabiting Carolinian forest throughout much of the eastern United States and southeastern Canadian provinces during the spring and summer months (Roth et al. 1996). The present study was conducted during the breeding seasons (May–July) of 2003 and 2004 at the Hemlock Hill Biological Research Area (HHBRA) in Crawford County, Pennsylvania (41°46'N, 79°56'W). The 100-ha study area was located within a 180-ha forest fragment composed of continuous mixed hardwood and hemlock forest and supported ~30 breeding pairs in both years.

We captured Wood Thrush using mist nets and banded them with a federal aluminum band and a color-band combination for individual identification. Previous studies of Wood Thrush territoriality suggest that the species exhibits a non-overlapping territory system (Twomey 1945). To determine the locations of territory boundaries, we initiated daily observations of male territorial interactions when males began returning to our study area in early May. Between 0530 and 1030 hours EST, we systematically walked the 50 × 50 m grid system located on the study area and mapped the locations of all male singing displays, chases among males, and countersinging events. These behaviors were used to interpret the locations of territory boundaries. Daily observations ceased once all females had initiated egg laying (20 May 2003; 21 May 2004). For the remainder of the breeding season, we opportunistically monitored territory boundaries while radiotracking and nest searching.

Radiotracking.—To examine territory use and male and female reproductive tactics, we fitted 22 social pairs with Holohil BD-2B (1.40 g) radiotransmitters (Holohil Systems, Carp, Ontario). Transmitters were attached using a figure-eight harness of embroidery thread looped through premanufactured holes in the transmitter (Rappole and Tipton 1991). Radiotracking sessions were conducted between 0600 and 1600 hours EST. Radiotagged social pairs were followed by two observers for 1-h intervals at a distance of approximately 20–30 m to avoid disturbance of normal behavior. In both years, there were cases in which only one member of the pair could be captured and fitted with a radiotag ($n = 6$) or in which unmated males were radiotagged ($n = 3$). These birds were also followed at 1-h intervals ($n = 60$ h) to document forays but were not included in our analyses, because it was difficult to distinguish pair forays from forays by individuals. Therefore, we observed radiotagged pairs over 196 tracking sessions. We excluded observations of a polygynous male and his two social mates and any observations collected when the fertility status of the female was unknown ($n = 37$ tracking sessions). We tracked 13 pairs during the fertile stage and 18 pairs during the nonfertile stage (Table 1). On average, pairs were tracked for 6.5 ± 3.5 h (range: 1–17 h) during the fertile stage, and 4.4 ± 2.5 h (range: 1–13 h) during the nonfertile stage.

TABLE 1. Forays and total time (h) tracked for each Wood Thrush social pair followed at Hemlock Hill Biological Research Area, 2003–2004. Total time each pair was tracked and number of pair, female, and male forays are shown for the fertile (F) and nonfertile (NF) nesting stages of the social female.

Year	Pair ID	Time tracked (h)		Number of pair forays		Number of female forays		Number of male forays	
		F	NF	F	NF	F	NF	F	NF
2003	CC19	4	0	0	–	0	–	0	–
	DD22	6	0	4	–	0	–	2	–
	V22	2	3	1	0	0	0	0	0
	V27	8	3	1	0	2	0	1	0
	Z19/CC25	15	13	2	0	0	0	0	3
	AA32	5	4	0	0	2	0	0	2
	DD26	7	6	0	0	0	0	0	2
	U18	0	1	–	0	–	0	–	0
	T24	0	3	–	0	–	0	–	0
	2004	DD33	1	4	0	0	0	0	0
V22		4	4	4	0	0	0	0	2
AA27		5	5	5	0	1	0	0	3
V28		0	1	–	0	–	0	–	0
EE21		10	5	2	0	0	0	0	2
V24		0	4	–	0	–	0	–	1
CC26		0	3	–	0	–	0	–	0
Z19		6	6	1	1	1	0	3	0
CC28		6	8	3	0	0	0	3	6
FF26		0	3	–	0	–	0	–	0
BB22		0	4	–	0	–	0	–	2

A territorial intrusion was documented if a bird moved >50 m into an area defended by a conspecific. Territories were located contiguously throughout the study area, and territorial boundaries abutted and were defended vigorously by males at the start of the breeding season. Because Wood Thrush territories do not typically exceed 2.8 ha (Roth et al. 1996), a 50-m movement onto a conspecific territory represents a substantial intrusion and provides a conservative estimate of off-territory foray rates in this species. Over our two years of observation, 33 territory intrusions (27%) were excluded from our foray analyses because they fell below this 50-m threshold and, by definition, occurred near territory boundaries. We used the total time members of a social pair were within 10 m of each other to estimate the duration of social-mate association as a potential measure of male mate-guarding (Davies 1992, Hanski 1992). We used visual observations, whenever possible, to confirm the location of social pairs. When we visually observed the pair, the male and female were typically within a few meters of each other, with the male perched above the foraging female. We also used the quiet *bup-bup* calls made by Wood Thrush males and females to reconfirm the locations of the radiotagged birds. At the distance (20–30 m) that we followed these birds, the combination of radiotag signal strength, vocalizations, and visual observations likely made the error in our estimate of location very low (a few meters).

We observed pairs over the female’s fertile (prebuild, build, lay) and nonfertile (incubation) nesting stages. The exact length of the fertile period is unknown for Wood Thrush, so we estimated

the female’s peak fertile period as five days before the start of egg laying and up to the day preceding the laying of the penultimate egg (Davies 1992, Mota and Hoi-Leitner 2003). This estimate is conservative, because female songbirds may be fertile up to 10 days preceding the start of egg laying (Birkhead 1998). The incubation stage was used as the nonfertile breeding stage with which to compare fertile behaviors. We could not find, capture, and fit social pairs with radiotransmitters before a female became fertile, because Wood Thrush initiate nesting activity almost immediately on arrival on the breeding grounds or following a failed nest attempt (Roth et al. 1996, M. L. Evans pers. obs.). Because females spend large portions of their time sitting on the nest during incubation, we limited our comparisons of female foray behavior and pair proximity between the fertile and nonfertile stages to the time that the female was off the nest.

Breeding synchrony.—The synchrony index of our study population was determined using the method outlined by Kempenaers (1993).

Parentage analysis.—We used five polymorphic microsatellite loci (Table 2) to genotype each individual. Loci were amplified using a touchdown polymerase chain reaction (PCR; Don et al. 1991). Products were analyzed using the fragment analysis application of a Beckman Coulter CEQ 8000 automated sequencer (Beckman Coulter, Fullerton, California). For each locus, we calculated the number and frequency of alleles and the expected (H_E) and observed (H_{Obs}) genotype heterozygosity. A significant discrepancy between observed and expected heterozygosity was detected for the $Cu\mu$ 05 locus, which suggests the presence of null alleles (Table 2). Null alleles may bias estimates of EPF (Ibarguchi et al. 2004). Therefore, we calculated the probability of resemblance (P_{Ra}) of the shared alleles in common between social father and offspring (Ibarguchi et al. 2004). Social fathers were excluded as the genetic parent if the cumulative probability of resemblance (P_{RaCum}) across all loci was >0.005 (after Ibarguchi et al. 2004). A parent–offspring pair with a P_{RaCum} value below this criterion has a <0.5% chance that the social male and offspring share alleles in common by random chance. Extrapair sires were also identified on the basis of this criterion.

Statistical analyses.—All variables departed significantly from a normal distribution (Shapiro-Wilk W test; $P < 0.05$), so non-parametric tests were used (Zar 1999). Factors influencing off-territory foray rates and duration of social pair association were investigated using generalized linear mixed models (GLMs) with Poisson (forays) and binomial (pair association) errors in GLMstat for Macintosh (Beath 2001). In the binomial model, the actual time social mates spent within 10 m of one another was used as the response variable and total time radiotracked was used as the binomial denominator. For the Poisson models, number of forays was the response variable. Time of day and female fertility status (i.e., fertile or not fertile) were included as covariates in all models, and pair or individual identity was included as a random factor to control for the partially paired structure of the data set. The occurrence of lone female forays over the fertile and nonfertile nesting stages was further investigated using a Wilcoxon signed-ranks test, because the GLM could not detect significant contributors to the response variable, likely because of the relatively modest numbers of lone female forays observed. For this test, we made use of repeated measures of a subset of females.

TABLE 2. Variability at five microsatellite loci among Wood Thrush sampled over the breeding seasons, 2002–2004.

Locus	t_m (°C)	Number of alleles	Fragment size range	N^c	H_E	H_{Obs}	P_R	$P(E)$
Dp μ 01 ^a	67–69	10	140–168	98	0.651	0.616	0.761	0.454
Cu μ 02 ^b	55–57	8	130–152	98	0.651	0.634	0.774	0.392
Cu μ 05 ^b	55–60	24	142–206	98	0.923*	0.604*	0.273	0.847
Cu μ 28 ^b	64.5–66	14	158–190	98	0.833	0.817	0.500	0.692
Cu μ 32 ^b	58–67	13	136–176	98	0.750	0.695	0.648	0.542
Cumulative							0.052	0.993

^aDawson et al. (1997).

^bGibbs et al. (1999).

^cNumber of unrelated adult Wood Thrush used in calculation of genetic variation.

*Statistically different ($\chi^2 = 9.464$, $df = 1$, $P = 0.002$). Definitions: t_m = annealing temperature, H_E = expected heterozygosity, H_{Obs} = observed heterozygosity, P_R = probability of resemblance (Ibarguchi et al. 2004), $P(E)$ = probability of exclusion (Chakraborty et al. 1988).

Statistical Package for the Social Sciences (SPSS), version 11 (SPSS, Chicago, Illinois), was used to conduct all non-GLM statistical tests. Results are reported as means \pm SD, and a significance level of 0.05 was applied throughout. All tests are two-tailed.

RESULTS

Forays.—Females frequently engaged in off-territory forays during the fertile nesting stage but they did not foray on their own for most of the observed forays (Fig. 1 and Table 1). For 74% (25 of 36) of off-territory forays conducted by females, their social mates were present. Off-territory forays by pairs were influenced by the fertility status of the female (GLM: F ratio = 30.55, $P = 0.0015$, $n = 20$), with pair forays occurring most frequently while the female was fertile (Fig. 1). Only one pair foray was observed during the nonfertile stage. The lone-female foray rate was also significantly higher during the fertile stage (Wilcoxon signed-ranks test, $Z = -2.023$, $P = 0.043$, $n = 11$; Fig. 1). In fact, lone females did not leave their territories when they were not fertile (Fig. 1; Tables 1 and 3).

Few lone males traveled off territory when their social mates were fertile (Table 3). The proportion of males who made solo forays increased when females were no longer fertile, but this change was not significant (Fisher's exact test, $P = 0.126$; Table 3). However, lone male foray rate was significantly higher during the nonfertile nesting stage than during the fertile stage (GLM, F ratio = 12.22, $P = 0.0007$ [fertility status]; F ratio = 16.08, $P = 0.0001$ [time-of-day]; $n = 20$; Fig. 1). During the nonfertile stage, male foray rate did not differ when the female was sitting on the nest or when she left the nest to forage (Wilcoxon signed-ranks test, $Z = -0.676$, $P = 0.499$, $n = 14$), so all observations of male forays during the nonfertile stage were pooled.

The increase in male foray rate during the nonfertile stage was not coincident with an increase in the number of females who were fertile in the surrounding population. Most females (85%) in this population were fertile simultaneously (synchronously breeding) during first broods. Breeding synchrony decreased to $\sim 30\%$ in subsequent nesting attempts, so the proportion of fertilizable females in the surrounding population actually decreased later in the breeding season, when males engaged in more frequent off-territory forays.

Territorial intrusions.—On our study site, Wood Thrush territories were, on average, 2.4 ± 0.8 ha (range: 1.5–4.0 ha) and

were arranged contiguously throughout the study area. Mean nearest-neighbor distance (distance between nests) was 90 ± 27 m (range: 50–150 m). The mean number of neighbors within 100 m of a Wood Thrush territory boundary was 5 ± 2 (range: 1–9 neighbors). The distances traveled by lone females and pairs indicated that they usually forayed on territories adjacent to their home territory (Table 3). However, the contiguous arrangement of territories in the study area would enable foraging Wood Thrush to encounter several conspecifics within a short distance. Pairs and lone females did not differ significantly in time spent off territory or in distance traveled off territory (Wilcoxon signed-ranks test, foray distance $Z = -1.187$, $P = 0.110$; percentage of time off territory, $Z = -1.580$, $P = 0.114$). In general, male Wood Thrush forayed farther and spent more time off territory when their social mates were not fertile than when their mates were fertile (Table 3). Male

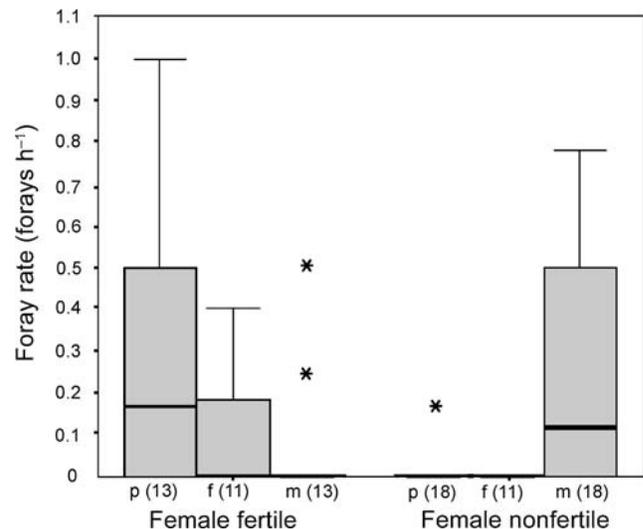


FIG. 1. Number of off-territory forays per hour exhibited by Wood Thrush pairs (p), lone females (f), and lone males (m) during the female's fertile and nonfertile nesting stages. Sample sizes are indicated in parentheses. Observations were collected over the breeding seasons of 2003 and 2004 between 0600 and 1600 hours EST. Box plots report median values; whiskers indicate 95% confidence intervals; asterisks indicate extreme values.

TABLE 3. Foray behaviors of Wood Thrush males, females, and pairs over the fertile (F) and nonfertile (NF) nesting stages of the social female. In the first row, number of individuals or pairs that forayed during each stage is shown. Mean distance traveled and mean time spent off territory during the 1-h tracking sessions are presented \pm SD and the range of observed values in each category is shown in parentheses.

	Females		Males		Pairs	
	F	NF	F	NF	F	NF
Number of individuals or pairs who forayed	4	0	4	9	9	1
Distance traveled (m)	113 \pm 125 (50–550)	0	67 \pm 29 (50–350)	95 \pm 39 (50–200)	104 \pm 56 (50–400)	50
Time spent off territory (min)	16 \pm 14 (1–60)	0	7 \pm 4 (1–15)	12 \pm 4 (2–33)	24 \pm 15 (4–60)	9

foray distances during the fertile and nonfertile stages demonstrate that they typically forayed to adjacent territories, regardless of their social mate's fertility status.

For all birds radiotracked over the two breeding seasons (including those later excluded from our analyses), we observed 123 forays. Most (120 of 123) of these forays were to areas defended by another Wood Thrush male. Although Wood Thrush tend to remain in the dense understory, we documented nine off-territory intrusions that resulted in visible interaction between the foraying individual, or pair, and the male defending the territory. We observed three lone-female forays that resulted in chasing events by the resident male. One observation of a pair foray resulted in an aggressive interaction between the pair and the resident male. Five males forayed onto neighboring territories during their social mate's incubation stage and were involved in aggressive chases with the resident male.

A few long-distance off-territory forays (>250 m) were conducted by pairs, lone females, and lone males over the course of the study, but they occurred relatively rarely. Only 17% (1 of 6) of forays by lone females, 17% (4 of 24) of forays by pairs, and 3% (1 of 32) of forays by males were >250 m (range: 300–2,200 m). All the long-distance forays occurred following a recent nest failure. In 60% (4 of 6) of cases, the foraying birds returned to their original territory to breed. In two cases, the female disappeared from the study area.

Social pair proximity.—Social pairs maintained a close physical association both on and off territory during the female's fertile stage. The percentage of time that socially paired males and females were within 10 m of each other did not differ significantly whether or not they were on their own territory (Wilcoxon signed ranks test, $Z = -0.420$, $P = 0.674$, $n = 10$). The fertility status of the female was the only significant predictor of the percentage of time males and females remained within 10 m of each other (GLM, F ratio = 17.80, $P = 0.0029$, $n = 21$). Overall, socially paired male and female Wood Thrush spent $90 \pm 10\%$ of their total time within 10 m of each other during the fertile stage of first broods (Fig. 2). When females began incubation and were no longer fertile, males and females decreased the percentage of time they spent together to $11 \pm 16\%$ (Fig. 2). While radiotracking, we occasionally observed Wood Thrush pairs from a distance, but because this species is sexually monomorphic, we usually could not determine which member of the social pair led pair movements or off-territory forays.

Parentage.—Fifty-one family groups were included in the analyses of parentage. Brood size averaged 2.96 ± 0.93 young per nest (range: 1–4). Six percent (9 of 151) of young were identified as extrapair, and 14% (7 of 51) of nests contained extrapair

young (EPY; Table 3). The number of EPY per nest did not differ significantly between years (Chi-square test, $\chi^2 = 1.566$, $df = 1$, $P = 0.457$), nor did the number of nests containing EPY ($\chi^2 = 0.722$, $df = 1$, $P = 0.697$). The number of EPY within a nest ranged from zero to two, but when EPY were detected, typically one nestling in the brood was the result of extrapair mating. For six of the nine EPY, the genetic father was identified (Table 4). Two of the extrapair sires defended territories adjacent to the male they cuckolded (distance between center of territories: 200 and 250 m), one extrapair sire defended a territory 650 m (three territories) away from the male he cuckolded, and one male's territory location was not determined in the year he cuckolded. Because Wood Thrush pairs may occasionally travel up to 2.2 km off territory during the breeding season, it is possible that this male and the unidentified extrapair sires may have inhabited areas outside the main study area.

We radiotracked 11 pairs during the fertile stage whose subsequent family groups were genotyped. Only one family group contained an EPY; therefore, we could not investigate a relationship between forays or pair proximity and rate of EPF.

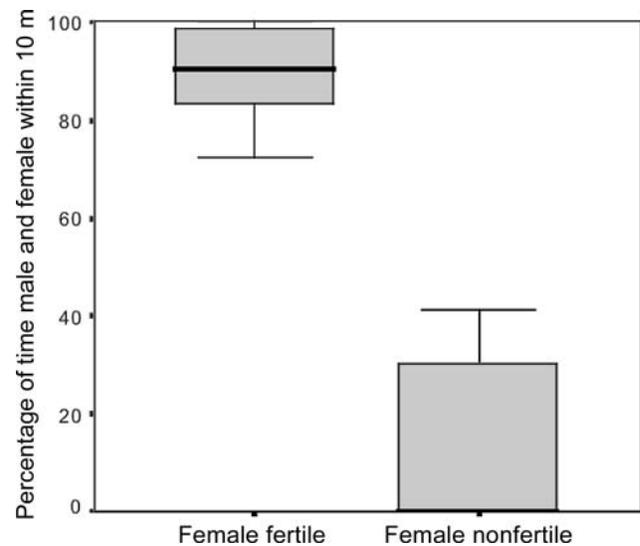


FIG. 2. Percentage of total time (on and off territory) socially paired male and female Wood Thrush spent within 10 m of each other during the fertile and nonfertile nesting stages of first broods. Box plots report median values; whiskers indicate 95% confidence intervals.

TABLE 4. Wood Thrush EPF at Hemlock Hill Biological Research Area, 2002–2004.

	2002	2003	2004	Total
Nests sampled	10	21	27	58
Nests used in analysis ^a (Young genotyped)	9 (29)	19 (56)	23 (66)	51 (151)
Nests with extrapair young (%) (Nests with extrapair young)	22.2 (2)	10.5 (2)	13.0 (3)	13.7 (7)
Extrapair young (%) (Number of extrapair young)	10.3 (3)	3.6 (2)	6.1 (4)	6.0 (9)
Extrapair young assigned sire (%) (Number assigned)	100.0 (3)	50.0 (1)	50.0 (2)	66.7 (6)

^aSome nests were excluded because of incomplete sampling of social parents.

DISCUSSION

Both male and female Wood Thrush forayed off territory in the present study. Independent male and female forays have been observed in other territorial passerine species (e.g., Hooded Warblers). However, we also observed frequent off-territory forays by social pairs. In fact, most of the off-territory forays we observed during the fertile stage were conducted jointly by males and females. Pair forays have been documented in a passerine extrapair mating system (Yellow-breasted Chat [*Icteria virens*]; Mays and Ritchison 2004), but observation of frequent social-pair forays is unprecedented. Off-territory forays have been suggested as a mechanism used by males and females to seek extrapair copulations (e.g., Birkhead and Møller 1992, Neudorf et al. 1997, Stutchbury 1998a, Double and Cockburn 2000). We did not detect high rates of EPF in our study population, despite these high levels of off-territory activity exhibited by males and females. However, our observations of frequent pair forays is in contrast to the independent forays typically observed in Common Yellowthroats, Hooded Warblers, and Acadian Flycatchers (species exhibiting high EPF rates; Neudorf et al. 1997, Stutchbury 1998a, Woolfenden et al. 2005, Pedersen et al. 2006). We suggest that within-pair interactions could also be playing a role in limiting EPFs in our study species.

Female forays.—In other avian species, observations of female off-territory forays during the fertile stage have been interpreted as evidence of a female mixed reproductive strategy, in which a female socially pairs with a male but also seeks matings with another male who may provide genetic or material benefits to her offspring (e.g., Sheldon 1994, Neudorf et al. 1997, Double and Cockburn 2000). Female Wood Thrush forayed only when fertile, which suggests that they were pursuing EPCs. However, alternative explanations for off-territory forays by females are also possible. For example, it has been suggested that females leave their territories in search of intraspecific brood-parasitism opportunities (Neudorf et al. 1997). In our study population, all 151 nestlings included in our genetic analyses were related to their social mother, which indicates that brood parasitism either does not occur or is extremely uncommon. It has also been suggested that fertile females foray for food or other resources that are not present on their own territories (Gray 1997). Fertile Wood Thrush females forayed short and long distances off

territory. Particularly during long-distance forays, females likely foraged. In forest-nesting songbirds, it has not been possible to obtain the direct observations necessary to exclude resource gathering as a possible function of forays. For many forest-nesting species, the use of radiotelemetry has been required to even detect the occurrence of off-territory forays (see Neudorf et al. 1997, Currie et al. 1998, Fraser and Stutchbury 2004, Woolfenden et al. 2005, present study). However, female foraging does not preclude EPCs as a possible explanation for, or risk of, off-territory forays.

Although female off-territory behavior in Wood Thrush did not result in frequent EPFs, these forays are still a likely mechanism resulting in the observed EPFs in this population. Wood Thrush females did not significantly change their off-territory behavior while foraging alone as compared with when they were accompanied by the social mate. Presence of males during off-territory forays may limit copulation opportunities but will not inhibit female assessment of other males in the population (Smiseth and Amundsen 1995). It is possible that the information gathered during pair forays assists females in choosing extrapair mates in future off-territory forays. Although four females forayed off territory alone while their fertilization potential was high, relatively few of the forays by females were solo (6 of 30). It is possible that this rate of lone female forays may not have been sufficient to produce extrapair young. Not all off-territory forays by females necessarily result in EPCs, and occasional EPCs may be overcome by more frequent copulations with the female's social mate.

Male forays.—Male Wood Thrush frequently forayed off territory with their social mates during the fertile period. However, lone male Wood Thrush engaged in few off-territory forays when their mates were fertile, especially compared with male Hooded Warblers (Stutchbury 1998a) and Acadian Flycatchers (Woolfenden et al. 2005). It is possible that the relatively low male-foray rates observed during the fertile stage reflect the lower overall fitness benefits obtained through this reproductive tactic, particularly when compared with other passerine species that regularly engage in EPF. Most male forays occurred once the social mate was no longer fertile and, in this highly synchronous population, when only a small proportion of potential extrapair females would even be fertilizable. Moreover, any fertile females encountered in this population are likely to be accompanied by their social mates. Foraging Wood Thrush males may also experience difficulty when attempting to locate extrapair females, because Wood Thrush females do not conspicuously vocalize while fertile, as female Hooded Warblers and Acadian Flycatchers do (Neudorf et al. 1997, B. J. M. Stutchbury unpubl. data).

Low levels of extrapair fertilization in Wood Thrush.—The level of EPF exhibited by Wood Thrush (6% of nestlings; 9 of 151) is remarkably low for a synchronously breeding Neotropical migratory passerine. On average, 32% of young in long-distance Neotropical migrants are extrapair and typically show a relatively high rate of EPF when compared with migratory passerines found in other geographic regions (e.g., Palearctic–African migrants, ~12% EPF; Stutchbury et al. 2005). Within North America, only the Blue-headed Vireo (*Vireo solitarius*) has a lower documented rate of EPF (~3%; Morton et al. 1998) than Wood Thrush. However, the Blue-headed Vireo arrives much earlier on the breeding grounds and exhibits low breeding synchrony and a much higher level of male investment in parental care (male incubation) than is

found in most Neotropical migrants. The Hooded Warbler, Common Yellowthroat, and Acadian Flycatcher have breeding ecologies more comparable to that of the Wood Thrush, yet these species exhibit higher rates of EPF (Hooded Warbler ~27%, Stutchbury et al. 1997; Acadian Flycatcher ~40%, Woolfenden et al. 2005; Common Yellowthroat ~26%, Whittingham and Dunn 2005). It is possible that this variation in the rate of EPF among species may be partially explained by differences in behavioral tactics (Griffith et al. 2002, Stutchbury et al. 2005). To investigate this possibility further, comparative studies of the behavioral tactics of males and females in species or populations exhibiting divergent levels of EPF are necessary.

Can pair proximity be interpreted as effective male mate-guarding?—The low levels of EPF observed in Wood Thrush may result if the close proximity between mates effectively functions as a male paternity-assurance tactic. Males spent ~90% of their time in proximity to their fertile social mates and, perhaps more importantly, accompanied their social mates off territory for almost three-quarters of the observed female forays. In Wood Thrush, this intense physical association occurred only while females were fertile. Birkhead (1979) has suggested that the close proximity of a social male during the female's fertile stage is a likely physical barrier to extrapair males. Under these circumstances, females that were accompanied by their social mates for all off-territory forays may have been completely prevented from interacting with extrapair males and, therefore, engaging in EPCs.

When the reproductive tactics of male and female Wood Thrush are compared with socially monogamous songbirds that exhibit high rates of EPF, this intense physical association between Wood Thrush males and females appears to be unique. In Hooded Warblers and Common Yellowthroats, fertile females regularly foray unguarded to adjacent territories (Neudorf et al. 1997, Fedy et al. 2002, Pedersen et al. 2006). Acadian Flycatcher males make long-distance off-territory forays, which result in EPFs, leaving their social mates unguarded (Woolfenden et al. 2005). All these species foray extensively off territory, yet only Wood Thrush exhibit very low levels of EPFs.

A few studies have suggested that even when males invest reproductive effort into mate guarding, this tactic does not prevent high rates of EPF (e.g., Gowaty and Bridges 1991, Kempenaers et al. 1992, Currie et al. 1998). However, most mate-guarding studies have been unable to follow foraging birds, so it is possible that overall guarding intensities exhibited by some species may be substantially lower than those exhibited on a male's own territory. Other studies have found a positive relationship between the mate-guarding effort of males and within-pair paternity (Krokene et al. 1996, Chuang-Dobbs et al. 2001, Brylawski and Whittingham 2004), which suggests that in some species, mate guarding is an effective paternity assurance tactic.

Wood Thrush breed in a temperate ecosystem in which large numbers of individuals breed during a restricted time period and may have many opportunities to interact with conspecifics that are also in breeding condition (Stutchbury and Morton 1995, Stutchbury 1998b). Moreover, we observed widespread off-territory forays over the course of this study. On the basis of these criteria, we would not have anticipated the low levels of extrapair mating observed in Wood Thrush. The prevalence of social-pair

association both on and off territory may be our best explanation for widespread genetic monogamy in this species. Wood Thrush may provide an excellent species in which to investigate how variation in male paternity-assurance tactics influences rates of EPF and female foray behavior. Future work on the efficacy of mate guarding in Wood Thrush should focus on experimentally manipulating the naturally high rate of pair association (also see Brylawski and Whittingham 2004). An experiment of this type is required to determine whether the close physical association observed in Wood Thrush social pairs is, in fact, effective male mate-guarding.

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