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Male Acadian flycatchers, *Empidonax virescens*, obtain extrapair fertilizations with distant females

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We used genetic parentage analysis and radiotracking to determine how far male Acadian flycatchers travel from their territory in search of extrapair matings. Acadian flycatchers on our study site have a linear spatial distribution of territories associated with watercourses. With this type of spatial arrangement, males have only one or two immediate neighbouring females within 100 m and therefore have limited opportunities for extrapair (EP) fertilizations unless they travel far from their territory. In our sample of 53 nests collected over 4 years, 58% of nests contained EP young and 40% of nestlings were EP young. We identified the EP sire and the location of his territory at 13 nests with EP young, and over half (7/13) were not immediate neighbours. The mean distance between the territory of the EP sire and the territory where he attained EP fertilizations was 526 m. We were also able to exclude all immediate neighbours as EP sires for 12 additional nests containing EP young. The minimum average distance between an EP sire's territory and the territory containing an EP young that he sired was estimated to be 910 m. Overall, the EP sire was a neighbour in only 24% of nests with EP young. Radiotelemetry observations showed that six of seven mated males made off-territory forays and averaged 0.4 forays/h. Males travelled an average of 202 m off-territory (range 50–1500 m) and were away from their territories an average of 10.2 min/foray. Because our findings contrast sharply with those of other studies examining extrapair fertilization in passerines, in which most extrapair sires are neighbours, we suggest that when males have few adjacent neighbouring females, the benefits of searching widely to increase the number of potential extrapair mates can outweigh the costs of EP forays.

Although the benefits of extrapair (EP) matings in birds are well understood for males (Trivers 1972; Westneat et al. 1990), the costs are less well known. The costs of seeking extrapair copulations (EPCs) can include the time, energy and risk of injury in making off-territory forays (Stutchbury 1998), energetic costs of advertisement to potential EP mates through displays (e.g. Mulder et al. 1994) or vocalizations (Hasselquist et al. 1996), the fitness costs of leaving their mate and territory unguarded while they seek EPCs off-territory (Westneat et al. 1990) and increased risk of predation. The costs of pursuing EPCs off-territory may be especially high for species that defend all-purpose territories compared with species where males

and females can aggregate away from nesting territories (e.g. Morton et al. 1990; Wagner 1992; Dunn & Robertson 1993; Dunn et al. 1994). With all-purpose territories, a male has contact with a limited number of females who are adjacent to his territory, and pursuing EPCs with additional females requires travelling greater distances, being off-territory longer, and trespassing on occupied territories to reach more distant females.

How far should a male travel in pursuit of EPCs off-territory? Paternity studies on passerines that defend all-purpose territories have found that extrapair sires are usually immediate neighbours (e.g. hooded warbler, *Wilsonia citrina*: Stutchbury et al. 1994, 1997; black-throated blue warbler, *Dendroica caerulescens*: Webster et al. 2001; great reed warbler, *Acrocephalus arundinaceus*: Hasselquist et al. 1995; yellow warbler, *Dendroica petechia*: Yezerinac et al. 1995). In hooded warblers, where male EPC behaviour has been studied with radiotelemetry, males make off-territory forays almost exclusively to adjacent territories (Stutchbury 1998). In the wheatear, *Oenanthe oenanthe*,

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most male intrusions occur early in the season and are made by males from adjacent territories (Currie et al. 1998). Males may focus their EPC effort on nearby territories because females are more likely to accept EPCs from familiar neighbouring males than more distant males, and/or because males are attempting to minimize the costs of making forays to encounter extrapair mates. When potential EP mates are evenly distributed, as is the case for hooded warblers and wheatears, males can make relatively short off-territory forays and still encounter many females on adjacent territories.

Here, we use genetic parentage analysis and radiotracking to determine the frequency of EP mating and movement patterns of males in a population of Acadian flycatchers that shows a linear arrangement of territories. Under this type of territory distribution, a male typically has only one or two adjacent territories and therefore faces a clear choice of remaining on or near his territory to minimize the costs of off-territory forays versus making forays to distant territories to encounter additional extrapair mates. If male Acadian flycatchers foray only on adjacent territories (i.e. they visit only 1–2 territories), they would have 66–84% fewer opportunities for extrapair paternity than males of species with an even or clustered territory distribution, with as many as six immediately adjacent territories (e.g. hooded warblers, B. J. M. Stutchbury, unpublished data). If minimizing the costs of forays is important in determining male EPC tactics, then male Acadian flycatchers should make forays primarily to adjacent territories and most EP sires should be neighbours. However, if the costs of making forays are low relative to the benefits of encountering a large number of potential EP mates, then male Acadian flycatchers should make forays to distant territories and most EP sires will not be neighbours.

METHODS

Field Methods

Acadian flycatchers are small, insectivorous, sexually monomorphic passerine birds (Whitehead & Taylor 2002). They nest in large tracts (<100 ha) of mature forest and are distributed widely throughout the available habitat in the eastern U.S. as far north as southern Ontario, Canada. We monitored Acadian flycatchers breeding at the Hemlock Hill Biological Research Area (41°N, 79°W), near Cambridge Springs, Pennsylvania, U.S.A. during four breeding seasons (1997, 2000–2002). Breeding territories at our study site are usually associated with streams and are not uniformly distributed within the forest plot. The study site (Fig. 1) contained seven streams and several areas of wet forest from which the springs emerged. The watercourses typically flowed from east to west and were separated by 400 m or more. Acadian flycatcher territories were arranged more or less linearly along the streams. The centres of adjacent territories were typically separated by 75–100 m and nests tended to be located near the centres of territories. In years of high breeding density, several territories that were not associated with streams were also occupied (Fig. 1d). We monitored a total of 135 territories over four breeding seasons (range 23–46 territories/year, mean $\pm$ SD = 34.0 $\pm$ 9.5). Twelve of these were occupied by unmated males, 120 by singly mated males and three by polygynous males.

Breeding territories at this site are traditional, with many territories occupied perennially regardless of the survival and/or return of past residents (Fig. 1a–d). Average territory size was approximately 1 ha. Annual breeding density on the study site ranged from 0.23 to 0.46 territories/ha (mean $\pm$ SD = 0.34 $\pm$ 0.09). Males began arriving on site in mid-May (earliest arrival 8 May) and females followed approximately 5–7 days later. The mean date of egg laying was 28 May (range 23 May–4 June). We captured birds using mist nets and banded all adult birds with a single USFWS aluminium band on one leg and a plastic, coloured leg band on the other, took a small blood sample (25–100 µl) via brachial puncture and measured (tarsus, wing length and mass) each bird. We visited each territory several times during the breeding season to determine occupancy, mated status and identity of the resident bird(s). We intensively searched the territories of mated males to locate nests. Nests were visited twice weekly to determine dates of nest initiation, hatch date, clutch size and fledgling success. When the nestlings were at least 5 days old we accessed the nest, banded and obtained a blood sample (25 µl) from each nestling. Approximately 50% of nests were depredated before nestlings reached 5 days of age.

We determined breeding synchrony of our study population in each of the 4 years (range 0.24–0.32; mean $\pm$ SD = 0.28 $\pm$ 0.03). The breeding synchrony index is calculated by determining the average percentage of females in the population that were fertile on the same day as the female in question. We defined the fertile period for a female as the period beginning 5 days before laying of the first egg and ending with laying of the penultimate egg (after Kempenaers 1993).

Genetic Analysis

We banded, sampled and genotyped a total of 90 adult males, 44 adult females and 154 nestlings over the four breeding seasons. The nestlings represented 62 family groups. We banded an average $\pm$ SD of 78 $\pm$ 11% of territorial males and 43 $\pm$ 13% of females in each year. Blood samples were stored at 4°C in 500 µl of Queen's lysis buffer (Seutin et al. 1991). DNA extractions involved cell lysis and the use of ammonium acetate and isopropanol to precipitate DNA (L. De Sousa, unpublished protocol) or 'Qiagen DNeasy Kit' (Qiagen Inc., Mississauga, ON). We used the allelic variation present at four hypervariable microsatellite loci to determine the paternity of each nestling. Two of these loci (EMIZ1, EMIZ27) were isolated from the least flycatcher, *Empidonax minimus* (Tarof et al. 2002) and two (SAP22, SAP32) were isolated from the eastern phoebe, *Sayornis phoebe* (Watson et al. 2002).

We amplified genomic DNA from each individual in a 10-µl PCR reaction containing 3.73 µl of water, 1 µl of
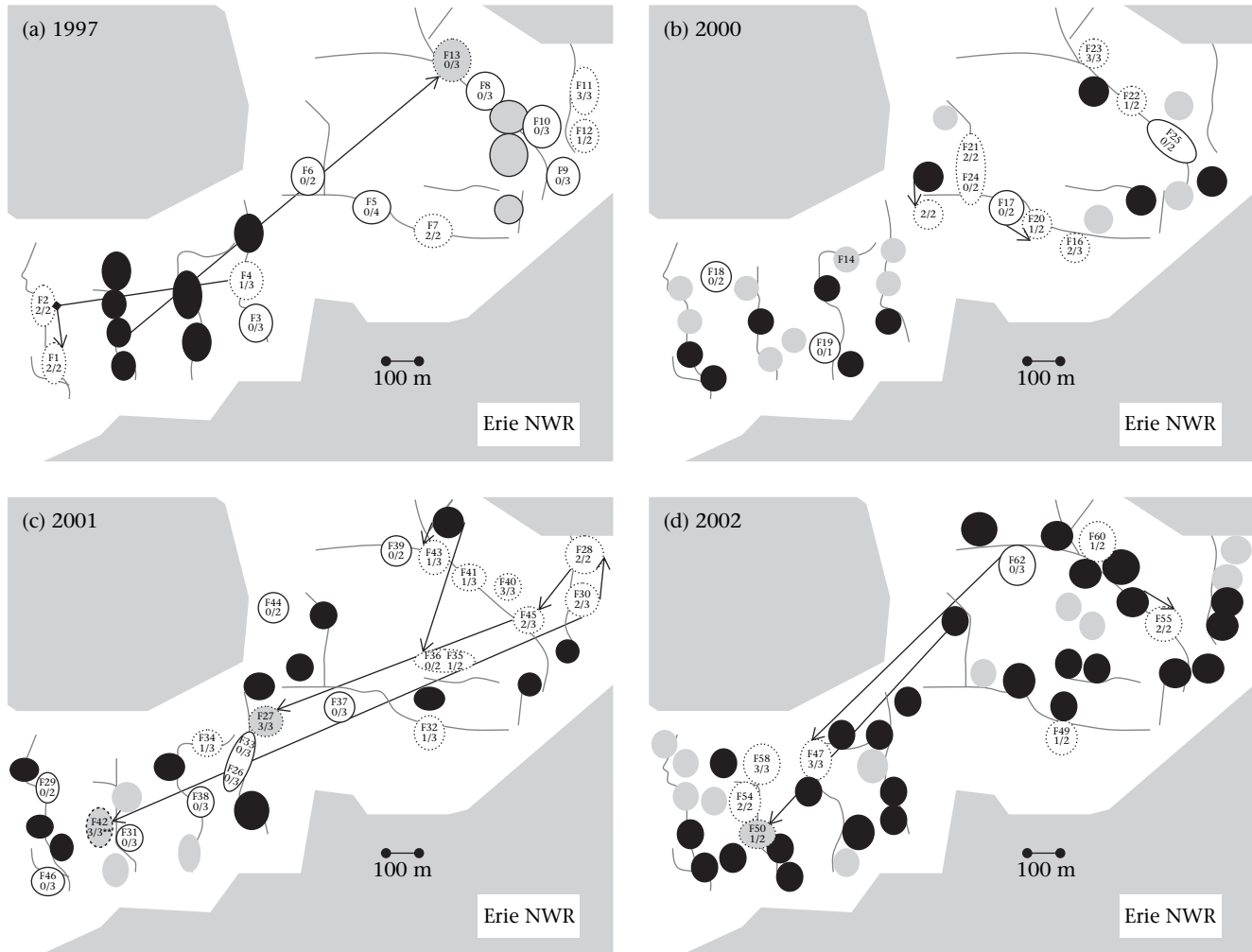
Figure 1. Schematic representations of the distributions of Acadian flycatchers in: (a) 1997; (b) 2000; (c) 2001; (d) 2002. Polygons represent the approximate size and locations of territories relative to water features (thick grey lines) and other territories (polygons). Black polygons indicate territories where the male was banded and sampled but the nest (if the territory holder was a mated male) was not. Grey polygons represent territories where the male was not banded and not sampled. Labelled polygons (i.e. F 12, 1/2) indicate territories where nests were sampled. The fraction indicates the proportion of extrapair (EP) young in the nest. For example, in family 12, one of the two sampled chicks was an EP young. Sampled territories with EP young are ringed with a dotted black outline and territories without EP young are ringed with a solid black outline. If an EP sire was identified, the EP male's territory is connected to the territory where he gained the EP fertilization by a solid black arrow. Grey shaded areas indicate areas of unsuitable habitat (agricultural fields, roads and housing).

PCR reaction buffer (Bio Basic Inc., Toronto, ON), 3.0 µl of 20 mM $MgSO_4$, 1 µl of BSA (Amersham Biosciences, Baie d'Urfe, PQ), 0.3 µl of 10 µM dNTPs, 0.03 µl of 10 µM forward primer, 0.06 µl of 10 µM reverse primer, 0.05 µl of 5 U/µl TSG (Bio Basic Inc.), 0.277 µl of radioactively labelled forward primer cocktail and 50 ng of DNA. The forward primer cocktail (per 30 samples) included 1.0 µl of 10 µM forward primer, 1.0 µl of 10 × polynucleotide kinase (PNK) reaction buffer (New England Biolabs Ltd, Pickering, ON) mixed with water in a ratio of 6:4, 3.0 µl of T4 PNK (New England Biolabs) and 1.0 µl of $\gamma^{33}P$-ATP (Amersham-Pharmacia). We incubated the labelled primer cocktail at 37°C for 30 min, then at 68°C for 10 min. PCR reactions were performed in an Applied Biosystems 9700 thermocycler using the following protocol. We performed an initial 2-min denaturing step at 94°C followed by 35 cycles of 20 s at 96°C, 20 s at the primer-specific annealing

temperature (EMIZ01 = 56°C, EMIZ27 = 59°C, SAP22 = 66°C, SAP32 = 61°C), and a 30-s extension step at 72°C, followed by a final 5-min extension step at 72°C. To visualize PCR products, each sample was run on a 6% denaturing polyacrylamide gel. Several positive (samples of known size) and negative controls were always included on each gel. After electrophoresis, gels were dried and exposed to autoradiograph film for 24–48 h. We scored the size of each PCR fragment by comparing bands to the reference samples run on each gel.

We calculated the frequency of each allele (χ_i) from the total population of adults genotyped ($\sum \chi_i = 1.00$), and calculated the expected frequency of heterozygotes ($h_e = 1 - \sum (\chi_i)^2$). We then compared the expected frequency of heterozygotes to the observed frequency of heterozygotes (h_o) and calculated the average probability of parental exclusion (P_e) for the four loci. This is the

probability, averaged over all alleles at a given locus, that a randomly chosen nonparental male will not possess the paternal allele belonging to a given offspring, given that the genetic mother is known (Jamieson 1994). The four loci were highly variable (12–37 alleles), showing high levels of observed heterozygosity (range 0.796–0.95) and high probabilities of exclusion (0.618–0.897). The cumulative exclusion probability, P(E) (Chakraborty et al. 1988) for the four loci was less than 0.0001, indicating that we could identify EP young and their sires with a high degree of certainty.

Genetic Parentage Analysis

We determined the genotypes of all individuals sampled and compared nestling genotypes with their social parents. Adults were excluded as putative genetic parents if the adult and nestling allele(s) mismatched by more than two base pairs at more than one locus. In family groups where the social mother was sampled ($N = 48$), 97% of the nestlings matched the female at all loci. In three cases, the nestling and female alleles differed by only one or two base pairs at one locus. These differences probably represent mutations or laboratory artefacts. A fourth case was the result of a data-recording error in the field. In three cases, the putative male parent mismatched the chick at a single locus. In two cases, the social father and the chick mismatched by only two base pairs, and in the third, both the chick and the father were homozygous but for different alleles. In all three cases, the father–chick pair matched at the other three loci. As with the female mismatches, these mismatches probably represent mutations or laboratory artefacts and so, in all three cases, the social male parent was presumed to be the genetic parent.

Since there was no behavioural or genetic evidence of intraspecific brood parasitism, we assumed that the social female was also the genetic female parent in all cases. We identified social male parents using field observations of nest defence and nestling feeding. We identified both social parents for 39 families, the female only for nine families and the social male only for 10 families. Using genetic analysis alone, we identified the female parent for three additional families where we were able to identify the female retroactively via her genotype (i.e. in these

cases we had been unable to capture the female the prior year).

Fifty-three of the 62 family groups we sampled are included in our analysis of EP mating by males (Table 1). To be included, a family group must have had either the social male identified and sampled ($N = 50$), or the genetic male parent identified as a male who was the social male parent of a family on another territory ($N = 3$).

Radiotracking

In 2001–2002 we attached radiotransmitters (Holohil Systems Ltd, Carp, ON, BD-2A transmitters, 0.75 g) to 10 adult males (six in 2001 and four in 2002). Radiotransmitters were attached to the birds using leg harnesses made from three strands of cotton embroidery thread (Rappole & Tipton 1991). In most cases, the mated status of the male was unknown at the time of capture, because females were still arriving and settling on territories. Of the 10 radiotagged males, nine were territorial. Of these, seven were mated and two were unmated but territorial. The final male was a floater who did not remain on or defend a discrete territory.

We followed males for 60–90-min observation sessions twice weekly for the duration of the battery life (2–4 weeks). We used a radio receiver (Wildlife Materials International, Inc., Murphysboro, Illinois, U.S.A.) and a hand-held three-element Yagi antenna. We began tracking birds 2 days after the radio was attached to allow the birds time to adjust to the transmitter. Tracking took place between 0700 and 1200 hours Eastern Standard Time, with variable start times for each male. Total tracking time was 58.5 h and averaged 5.9 h (range 3–9 h) per male. If a male left his territory during a tracking session, we followed him as closely as possible and recorded the distance and duration of the off-territory foray. Interactions with other birds, conspicuous behaviours and vocalizations were also recorded. We defined off-territory forays of males as movements of more than 50 m outside the territory boundary of a focal male. We recovered the radiotag from one of the 10 males. The remaining tags probably fell off before the male's departure from the study site in the autumn. Three of the 10 radiotagged males returned to the study site the next year.

Table 1. Frequencies of extrapair (EP) young across years and success at identifying EP sires

Year	Nests	% Nests containing EPY (N)	% EP nests with EP sire identified (N)	Number of chicks sampled	% EP young (N)	% EP young with sire identified (N)
1997	13	54 (7)	43 (3)	35	34 (12)	42 (5)
2000	11*	55 (6)	100 (6)†	23	48 (11)	64 (7)†
2001	21	52 (11)	55 (6)	56	38 (21)	52 (11)
2002	8*	88 (7)	29 (2)	19	53 (10)	50 (5)
Total	53	58 (31)	55 (17)	133	41 (54)	53 (28)

*One of 12 nests in 2000 and eight of 16 nests in 2002 were excluded because we were unable either to identify and sample the social male mate or to identify the sire.
†In 2000, five EP young from four nests were sired by males that were identified and sampled in the year $n + 1$, and determined to be the EP sire in the final genetic analysis; therefore, the territorial status and location of these males in year n were unknown.

Frequency of EP Matings

The average $\pm$ SD brood size was 2.5 ± 0.6 nestlings (range 1–4). Thirty-one (58%) of the 53 nests included in the EP paternity analysis contained extrapair young (EPY). Fifty-four (41%) of the 133 nestlings were sired by a male other than the social male parent. We identified the EP sire for 28 (53%) of these 54 offspring (Table 1).

The proportion of EPY in each nest ranged from 0 to 1.0: nine nests contained a single EPY, 13 nests contained two EPY and six nests contained three EPY. We identified the EP sire for at least one of the EPY in 13 of the nests that contained two or more EPY. In eight cases, a single male was the father of all EPY, and in the remaining five cases there were at least two EP sires for offspring in the same nest.

Locations of EP Sires

Using the results of the parentage analysis, we were able to identify the EP sire at 17 nests (Table 1). Based on field observations we knew the locations of the territories of 13 of these males. The remaining four males were identified as EP sires of nests in 2000 but were not banded and sampled until the following year. Since they were among the unbanded males in 2000, the location of their territories in that year was unknown. Of the 13 remaining nests for which the location of the EP sire's territory was known, six EP sires were neighbouring males. We defined a neighbour as a bird on a territory directly adjacent to and on the same stream, or within 100 m of the focal territory (for territories located between streams). The mean $\pm$ SD distance between territories of the EP sire and the cuckolded nests was 526 ± 447 m (range 50–1425 m). When we excluded the data from the six nests where a neighbouring male was the EP sire, that distance increased to 656 ± 416 m.

Although we did not identify the EP sire of all of the nests containing EP young, we were able to infer that the EP sire was not a neighbour for nests on territories where all neighbouring males were sampled ($N = 13$). For this second set of data we assumed that the unidentified EP sire was an unsampled resident male. Therefore, the

Table 2. Number of nests containing extrapair (EP) young for which the sire was identified or all neighbouring males were identified and sampled, and the status (neighbour/non-neighbour) of the EP sire

Year	EP sire identified	Number of nests for which all neighbours were sampled	Number of EP sires that were	
			Non-neighbours	Neighbours
1997	3	4	6	1 (14%)
2000	2	0	0	2 (100%)
2001	5	6	9	2 (18%)
2002	3	2	4	1 (20%)
Total	13	12	19	6 (24%)

distance between the territories with EPY and the nearest territory with an unsampled, resident male served as an estimate of the minimum distance between territories of these EP sires and the nests they cuckolded. The average $\pm$ SD distance was 910 ± 641 m (range 300–1800 m), which did not differ significantly from the distances calculated using the EP sires that we identified through the genetic analysis (two-tailed t test: $t_{21} = -1.11$, $P = 0.278$).

To summarize, for a total of 25 nests we either identified the extrapair sire, or sampled all of the neighbouring males and excluded them as putative parents using the genetic analysis. Overall, the EP sire was a neighbour in only 24% of these nests (Table 2).

Off-territory Forays

In 58.5 h of radiotracking, we detected 21 off-territory forays during 14 of the 35 radiotracking sessions (Table 3). The two unmated males did not leave their territories at all during 10.5 h of tracking. In contrast, six of seven mated males made off-territory forays during the tracking sessions (total 44 h), with a mean $\pm$ SD foray rate of 0.42 ± 0.62 forays/h (range 0–2.7) (Fig. 2a, b). Only one mated male did not make any off-territory forays during his tracking sessions. The floater ranged widely during the 4 h that we tracked him. He was on a different area of the study site each day he was tracked (Fig. 2a) and he left the

Table 3. Summary of off-territory forays by radiotracked Acadian flycatcher males during the 2001–2002 breeding seasons

Male	Tracking hours	Total forays	Mean foray distance (range, m)	Mean foray duration (range, min)	Cuckolded
92114	3	0			Not sampled
92128	3	3	533 (50–1500)	25 (5–60)	Not sampled
92267	5	1	50	3	Yes
92122	6	2	525 (50–1000)	51.5 (45–58)	Yes
92271	5	0			
17032	5	0			
17352	9	11	86 (50–200)	4.4 (1–7)	Not sampled
98216	9	4	100	7.5 (5–7)	Not sampled
17355	9	3	116 (50–100)	5 (2–13)	Yes
Overall mean $\pm$ SD	5.9 $\pm$ 2.4	0.4 $\pm$ 0.6	202 $\pm$ 361	10.2 $\pm$ 19.4	

Figure 3. Relationship between foray distance (m) and duration (min) for males whose mates were fertile (●) and not fertile (i.e. incubating: △).
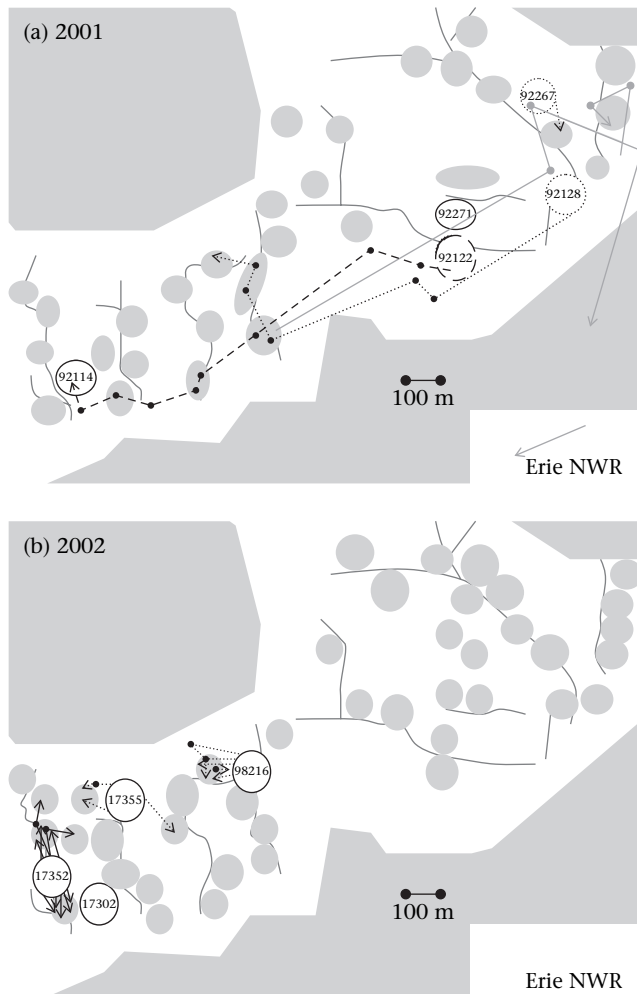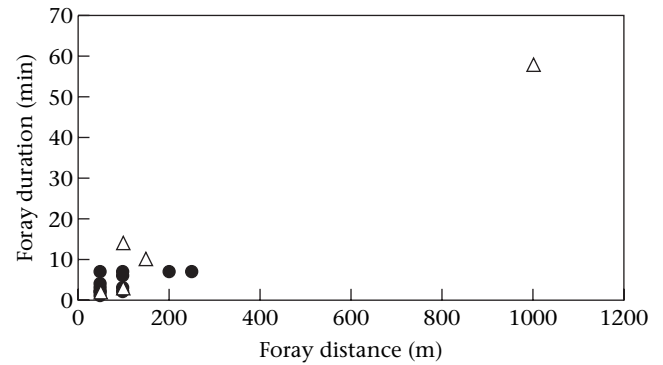
Figure 2. Schematic representations of the off-territory forays of Acadian flycatcher males radiotracked in (a) 2001 and (b) 2002. Polygons represent the approximate size and locations of territories relative to water features (thick grey lines) and other territories (polygons). White polygons indicate territories where the male was radiotracked. Arrows indicate the approximate paths and distances travelled by males during off-territory forays. Each bird is represented by a different line type (solid, dotted, dashed). The locations and movements of the floater male (in 2001) are indicated by thin grey lines with arrows. Each tracking session is represented by a separate arrow. Labels indicate male band numbers. Grey shaded areas indicate areas of unsuitable habitat (agricultural fields, roads and housing).

study site (moved to the nearby Erie National Wildlife Refuge) 14 days after we attached the radiotransmitter.

Males travelled an average $\pm$ SD of 202 ± 361 m off their territories during forays. Males visited potential extrapair mates 50–1500 m away within the forest (Fig. 2a). In six of 21 forays (50%), males visited nonadjacent territories and intruded on an average of three different territories (range 1–6) before returning to their home territories. The mean $\pm$ SD duration of forays was 10.2 ± 16.5 min (median = 6 min). Regression analysis indicated that there was a significant linear relationship between foray distance and duration (duration = $1.26 \times$ ((distance) + 0.04); $R^2 = 0.94$, $F_{1,20} = 9.51$, $P = 0.008$)

(Fig. 3). Forays to neighbouring territories lasted less than 8 min, whereas forays to non-neighbours lasted 8–60 min.

Radiotracking observations showed that males visited both adjacent and nonadjacent territories regardless of the fertility status of their social mate (Fig. 3). Furthermore, in seven of the 13 cases in which we had identified the EP sire of an EP nestling, we knew the nest stage of the EP sire's social mate on the date that the EP female mate laid the first egg of her clutch. In 29% of these cases ($N = 2$) the female mate was fertile, indicating that males gained extrapair fertilizations (EPFs) while their social mates were fertile.

Most direct observations of radiotagged males during off-territory forays proved difficult because the birds either remained high in the canopy, moved surreptitiously, or did not vocalize. Thus, had these males not been radiotagged, their absences from their own territories and their territorial intrusions would not have been detected. However, there was one exception to this general pattern. We frequently observed the single floater male chasing females during territorial intrusions, interacting with territorial males and vocalizing during tracking sessions. Only four interactions with other birds were observed during tracking sessions. Two were male–female interactions and two were male–male interactions. These included two intrusions on territories of radiotagged males while they were being tracked, a single copulation between a radiotagged male and his mate on their territory and a male–female interaction between a radiotagged male and a female while the male was intruding on the female's territory.

Neither the floater male nor any of the other nine radiotagged males were identified as an EP sire of any sampled offspring. However, because of nest predation, we were only able to sample offspring from five of the 15 territories known to have been visited by these males. We sampled the nestlings and the female associated with the nest on the territories of three of the radiotagged males and all three males were cuckolded (Table 2). Two of the males sired none of the three young in their own nests and the other male sired two of the three young in his own nest.

DISCUSSION

The aim of our study was to examine the relative importance of the costs and benefits to males of pursuing

extrapair mates when territories are unevenly distributed in space. The results of our genetic analysis demonstrate that male Acadian flycatchers frequently gained EP young with females that were not on neighbouring territories. Radiotracking results showed that males made frequent off-territory forays to neighbouring territories and to territories up to 1500 m away. These findings contrast sharply with those of other studies, in which most extrapair sires are adjacent neighbours (Hasselquist et al. 1995; Yezerinac et al. 1995; Stutchbury et al. 1997; Webster et al. 2001). We suggest that when males have few adjacent neighbouring females, they opt to search widely for EP opportunities rather than focus their EP effort on a small number of nearby females. For this tactic to be successful, the costs to males of making forays to non-neighbouring territories must be relatively low compared with the benefits of encountering distant females (e.g. females accept EPCs from distant males).

Off-territory Forays

We assume that mated males make off-territory forays to obtain EPFs. Several lines of evidence indicate that forays are a male tactic to pursue EP mating opportunities. First, all but one of the mated males that we tracked were observed making off-territory forays. Mated males on average, made off-territory forays once every 2 h, but we did not observe a single off-territory foray by an unmated male. If forays are related to foraging, we would expect to see similar rates of forays by all males regardless of their mated status. Second, during forays, males were surreptitious and did not vocalize, perhaps to avoid detection by the territory owner (e.g. Stutchbury 1998). During 44 h of radiotracking, we observed only two aggressive interactions between territory owners and intruding radiotagged males. In contrast, the floater male was observed chasing females, interacting with the territorial male and frequently vocalizing during all of the territorial intrusions documented, suggesting that he was trying to gain a territory. We observed only two copulation attempts by mated males making forays, but this is not surprising given that these males were surreptitious and copulation behaviour, within mated pairs, was rarely witnessed. We observed only one within-pair copulation, which involved a radiotagged male and his mate. Finally, in 67% of cases ($N = 14$), males intruded on territories where the female was fertile, although, on average, only 28% of females were fertile on a given day. How a male can determine the fertility status of a distant female remains unknown.

The costs to males of making EPC forays include the risk of cuckoldry as a result of a male being absent from his social mate and territory (Westneat et al. 1990) and the energetic costs and risk of injury when caught trespassing on neighbouring territories (Stutchbury 1998). In Acadian flycatchers, the main cost of longer-distance forays appears to be the time males are absent from their territory. Since 58% of broods contained EP young, there could be a high risk of cuckoldry for males that leave their mate for long periods. Radiotracking data indicated that two of three radiotagged males that were cuckolded made forays while

their social mates were fertile. In some species, the male rarely makes EPC forays while his own mate is fertile (Westneat et al. 1990; Currie et al. 1998). In contrast, male Acadian flycatchers frequently made EPC forays even when their own mates were fertile, suggesting that mate guarding does not limit a male's opportunity to seek EPCs.

Male Acadian flycatchers that trespassed on other territories did not appear to incur a significant cost, because we rarely saw aggressive male–male interactions during territory intrusions. During 44 h of radiotracking we saw only two aggressive male–male interactions during off-territory forays (9% of 21 forays). This value is lower than that observed for hooded warblers, where male–male chases and aggression occur in 20% of forays (Stutchbury 1998), and for wheatears, where 80% of male intruders are chased early in the season (Currie et al. 1998). The risks of trespassing may be lower in Acadian flycatchers because they live in forested stream habitat where light intensity is low, their plumage is dull and sexually monomorphic, and the clandestine behaviour of intruders makes them difficult for residents to detect. Furthermore, while making very long forays, male Acadian flycatchers at our study site moved through unoccupied, and therefore, undefended areas on their way to distant territories (Fig. 2a). However, if territories were evenly spaced and close together, males on long forays presumably would encounter defending territorial males along their entire route.

Although no comparable data exist for Acadian flycatchers having clumped territories, a direct comparison with hooded warblers illustrates the differences in extrapair behaviour that we suggest are linked to the spatial distribution of territories. We chose hooded warblers for comparison because they defend all-purpose territories at our study site and are the only species for which comparable data are available (Stutchbury et al. 1997; Stutchbury 1998). Levels of extrapair paternity are high in both species and males pursue EPCs with similar frequency (0.4 forays/ h). Male hooded warblers intrude primarily on neighbouring territories 75 m away and are off their own territory, on average, 6–7 min/foray. In contrast, Acadian flycatchers in our study travelled, on average, over 200 m away from their territories, half of their forays were to non-neighbouring territories and males were off-territory, on average, 10 min/foray. Finally, whereas almost all hooded warbler EP young are sired by neighbours, only 22% of Acadian flycatcher EP young in our study were sired by neighbours. This difference is likely to be due to the fact that male Acadian flycatchers must travel further off-territory to gain access to similar numbers of potential EP mates. Within a 75-m radius of a focal territory, a hooded warbler male can potentially access between four and six territories (B. J. M. Stutchbury, unpublished data). Male Acadian flycatchers need to travel over 200 m from their territories to access a similar number of territories.

Why Do Females Accept EPCs from Distant Males?

Female birds are no longer viewed as passive recipients of male EP mating efforts due to evidence of females

advertising their fertility status (Stutchbury 1998), seeking EPCs (Kempenaers et al. 1992; Neudorf et al. 1997; Double & Cockburn 2000) and the benefits of EP mating to females (reviewed by Hasselquist & Kempenaers 2002). It is possible that female Acadian flycatchers make off-territory forays, but additional radiotelemetry would be required to document this behaviour. Most other studies of socially monogamous passerines have found that the extrapair sire is usually a neighbouring male (Hasselquist et al. 1995; Yezerinac et al. 1995; Stutchbury 1998; Webster et al. 2001). For these species, because of their even spatial distribution, females choose a genetic mate from a relatively limited pool of possibilities (i.e. immediate neighbours), and females may be able to assess the relative quality of visiting males due to their proximity.

In contrast, female Acadian flycatchers may be able to choose from a much larger pool of EP mates because males travel so far in search of EP mates. On average, EP sires fathered young on territories 526 m away from their home territories. In this population, a female Acadian flycatcher could have as many as 22 potential mates within this radius (see territory F54, Fig. 1d). However, many of these potential males may be unfamiliar since they occupy nonadjacent territories. If females can and do assess male quality through behavioural interactions, singing or displays, then neighbour males should have an advantage over distant males in gaining EPFs. But this does not appear to be the case for Acadian flycatchers. If the benefits of EPCs to females include genetic diversity or fertility insurance, then females may not need to consider male quality or familiarity when choosing EP mates. But, if female benefits from EP mating are related to 'good genes', how do females assess the quality of unfamiliar males with whom they do not frequently interact? Perhaps males advertise to distant females using a long-distance signal like dawn song, which may be heard up to 500 m away (personal observation). Male Acadian flycatchers are one of the first species to begin singing during dawn chorus (0530 hours Eastern Standard Time) and females may be able to use dawn song as a long-distance signal to assess potential EP mates. We often observed males countersinging with neighbours at territorial boundaries while singing dawn song.

This study helps to explain why breeding density is not a good predictor of extrapair paternity in comparisons between species and within species (reviewed by Griffith et al. 2002). Although it makes intuitive sense that high density should result in a higher encounter rate between potential extrapair partners and therefore result in high EP paternity (Westneat & Sherman 1997), our study shows that male EP behaviour can overcome a low density of territories. In the case of Acadian flycatchers, males have close adjacent territories but nevertheless seek and obtain EPFs on distant territories. The costs of making long-distance forays may not be as high as previously thought, especially for species in which males do not guard their mates closely and in which females accept EPCs from non-neighbouring males. Acadian flycatchers do have evenly spaced territories in other parts of their breeding range (Whitehead & Taylor 2002), making it possible to test whether the extrapair mating system in those populations involves forays and extrapair fertilizations among adjacent territories.

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