Extraterritorial forays are related to a male ornamental trait in the common yellowthroat

MARC C. PEDERSEN, PETER O. DUNN & LINDA A. WHITTINGHAM

Department of Biological Sciences, University of Wisconsin-Milwaukee

Despite numerous studies of extrapair paternity in birds, little is known about the behaviours that males and females use to seek (or avoid) extrapair copulations. We used radiotelemetry to examine the extraterritorial movements of both male and female common yellowthroats, *Geothlypis trichas*, in relation to male ornaments, particularly the black facial mask. We found that many males (62%) and females (47%) forayed, and they primarily visited the territories of immediate neighbours (91%). Parentage analyses revealed that the majority of extrapair sires were neighbours (80%) who typically had larger facial masks than the male that they cuckolded. Females only forayed during their fertile period, and they directed most of their forays to territories of males with larger masks than their own social mate. In contrast, males directed most of their forays to territories where the female was fertile and the resident male had a smaller mask than their own. The relatively short foray distances of birds may be partly responsible for the wide distribution of extrapair fertilizations among males in the population (45% of males). If this is a general pattern among species, then the effect of extrapair mating on sexual selection is likely to be weaker than currently thought.

Sperm competition is widespread in animals with biparental care, and it often results in several males siring young in a brood (Birkhead & Møller 1992). In birds, these cases of multiple paternity can arise from extrapair copulations between males and females on nearby territories (Griffith et al. 2002), while in fish, multiple paternity can result from males that adopt specialized tactics (sneakers and satellites) to cuckold territorial males that defend nests and provide parental care (e.g. Jones et al. 2001; Neff 2001). Multiple paternity has interesting evolutionary consequences because it has the potential to dramatically increase the intensity of sexual selection in socially monogamous species (Webster et al. 1995).

Although a large number of studies have documented multiple paternity, we still know little about how it arises. In particular, it is often unknown if one or both sexes leave their territories to seek copulations with extrapair partners. As a consequence, we do not know whether patterns of extrapair fertilization are primarily due to female choice or male–male competition (Westneat 2000) and how interactions with potential extrapair mates produce sexual selection on male ornamental traits.

Numerous authors have suggested that females choose to mate with extrapair males displaying more extravagant ornaments, but it is also possible that more ornamented males are more successful because they are superior competitors with other males (e.g. in terms of maximizing their paternity with their social mate or attracting extrapair mates; Westneat & Stewart 2003). Thus, very little is known about how male and female behaviour leads to a correlation between male ornamental traits and extrapair fertilization success.

It is possible that males with larger ornaments have more time and energy for pursuit of extrapair copulations, in which case they may make more visits to females on other territories or intrude more often onto the territories of males with smaller ornaments. This would suggest that selection on ornament size comes from male–male competition. On the other hand, female choice may act on ornament expression if females prefer males with larger ornaments and leave their own territory to seek extrapair copulations on the territories of males with larger ornaments. Both of these processes could occur simultaneously, and since extrapair fertilizations involve the female, pair male and extrapair male, we might expect complex and conflicting interactions with variable effects on sexual selection (Westneat & Stewart 2003). For example, these two processes of sexual selection could act in concert or in opposition on male ornamental traits. Both

Correspondence: P. O. Dunn, Department of Biological Sciences, University of Wisconsin-Milwaukee, P.O. Box 413, 3209 N. Maryland Avenue, Milwaukee, WI 53201, U.S.A. (email: pdunn@uwm.edu).

theoretical and empirical studies suggest that females often prefer male ornaments that are also used in male–male interactions (reviewed by Kodric-Brown & Brown 1984; Berglund et al. 1996), but there is also increasing evidence that female choice and male–male competition produce opposing selection on male traits (e.g. Forsgren 1997; Candolin 2004; Wong 2004). How these forces operate will ultimately determine the strength of sexual selection on male traits.

There are several questions about extrapair mating behaviour that have rarely been examined in detail. First, do both males and females pursue extrapair copulations off their territory? Studies show that males (Stutchbury 1998; Woolfenden et al. 2005) as well as females (Double & Cockburn 2000) foray off their territories; however, it is often unclear whether male or female forays (or both) result in extrapair copulations. For example, male superb fairy-wrens, *Malurus cyaneus*, often make highly visible forays off their territories to display to neighbouring females, but they rarely engage in extrapair copulations during these visits. Instead, extrapair copulations occur in the dark before dawn when females leave their territories to visit males (Double & Cockburn 2000). Second, do more ornamented males pursue extrapair copulations more vigorously than less ornamented males? Lastly, do females visit extrapair males that are more ornamented? We studied these questions using radiotelemetry of common yellowthroats, *Geothlypis trichas*, a species in which the size of a male ornamental trait (black facial mask) is related to extrapair fertilization success (Thusius et al. 2001b). This small (10–11 g), socially monogamous songbird has substantial levels of extrapair fertilization (46% of broods contain extrapair offspring; Thusius et al. 2001b). Males possess three ornamental traits that vary in size among individuals: a black facial mask, a greyish-white border above the mask and a yellow bib (throat, breast and belly). In a previous study, males with larger masks arrived earlier on the breeding grounds and were more likely to gain social and extrapair mates (Thusius et al. 2001b). Although mask size also appears to increase with breeding experience (i.e. age), even experienced males were more likely to gain extrapair paternity when they had a larger mask (Thusius et al. 2001b), and experimental manipulations of mask size in the aviary also revealed that females preferred males with larger masks (Tarof et al. 2005). Here we examined the extrapair mating tactics of both males and females in relation to the size of all three male ornaments and the colour (hue, saturation and brightness) of the bib.

METHODS

Study Area and Species

We studied common yellowthroats at the University of Wisconsin-Milwaukee Field Station in Saukville, Wisconsin, U.S.A. (43°23′N, 88°01′W). In 2002 and 2003, there were 28 and 36 territories, respectively, located in 5.4 ha of contiguous conifer bog and sedge marsh. The study area was marked by a grid system divided into 25-m quadrants to facilitate mapping of bird locations. Males settled on territories in early May; females arrived 3–10 days later

than males (Thusius et al. 2001b). Females build the nest and incubate the eggs (4–5 per clutch), while both sexes feed the young (Guzy & Ritchison 1999). Territory boundaries were determined and mapped through daily surveys.

Morphological Measurements and Male Ornaments

Adults were captured using mist nets and fitted with a unique combination of coloured leg bands. We measured wing chord, tail length, tarsus length (to the nearest 0.1 mm) and body mass (to the nearest 0.1 g) for all males and females. Males banded on the study area in previous years were considered to have previous breeding experience. The total size of the facial mask, mask border and yellow bib was measured using image analysis software following Thusius et al. (2001b) and Tarof et al. (2005). Repeatability (Lessells & Boag 1987) of these size measurements was high for different images of mask ($r = 0.93$), mask border ($r = 0.94$) and bib ($r = 0.99$).

We used Adobe Photoshop Elements 2.0 (Adobe Systems 2002, San Jose, California, U.S.A.) to estimate the hue, saturation and brightness at nine locations on digital images of the bib (see Tarof et al. 2005 for more details). We entered these three variables into a principal components analysis (PCA) to yield a single bib colour score (PC 1) that was used in the analyses. The first principal component explained 50% of bib colour variation and loaded positively for hue and brightness and negatively for saturation.

Radiotelemetry

Both the male and female of a social pair were outfitted with BD-2A (0.75 g) or BD-2N (0.53 g) radiotransmitters (Holohil Systems, Carp, Ontario, Canada). Transmitters were attached around the legs using a figure-eight harness (similar to Rappole & Tipton 1991) made of 0.8-mm-thick elastic bead cord from which the fabric covering was removed. Two loops (each 1 cm) were glued together with superglue (cyanoacrylate) to form the harness, which was then glued to the transmitter. The use of elastic loops allowed easy attachment to the bird and prevented chafing around the legs. After attachment, the transmitter rested on the rump and the antenna extended along and beyond the tail feathers. The transmitter and harness were 4.7–6.7% of the average adult mass (11.3 g) and were removed from the birds after the battery life expired (21 days).

Males and females were radiotracked during the fertile period and early incubation (nonfertile period). Females typically build the nest in 4–5 days (Guzy & Ritchison 1999), so we conservatively defined the female's fertile period to be nest building through the day that the penultimate egg was laid (Neudorf et al. 1997). We attached transmitters to males and females 2–3 days before the onset of nest building, and in both years we radiotracked individuals between 0430 and 1200 hours (Central Daylight Time) because most passerines copulate in the early morning (Birkhead & Møller 1992). In 2002 we also tracked individuals between 1200 and 1900 hours because extrapair

copulations may occur later in the day (Venier et al. 1993; Hanski 1994), but no forays occurred after 1230 hours.

We collected a total of 368 h of telemetry data from 28 birds (13 pairs and 2 individual females). Radiotracking sessions each lasted 2 h and typically focused on simultaneous tracking of one pair by one observer. Most pairs were tracked at least seven sessions ($\overline{X} \pm SE = 7.8 \pm 1.2$) during the fertile period and five sessions (5.7 ± 1.5) during the nonfertile period (days $1-3$ of incubation). All females ($N = 15$) were tracked during their fertile period, and eight of those females were also tracked during their nonfertile period. We tracked individuals using a Communications Specialists R-1000 or Wildlife Materials TRX-1000S receiver attached to a hand-held Yagi directional antenna. The locations of each individual were recorded every minute onto maps in relation to grid markers (25×25 m) and territorial boundaries on the study site. We defined an extraterritorial foray as any movement by the male or female that extended at least 10 m inside another territory (average territory diameter = 45 m; Thusius et al. 2001a). All extraterritorial movements, interactions between individuals, foraging behaviour and vocalizations were recorded ad libitum during the 2-h tracking sessions. There was no difference between the ornament sizes of radiotracked males and other males in the study area (all $P \geq 0.14$).

Microsatellite Analyses of Parentage

To relate extraterritorial behaviour to extrapair fertilization success, we collected blood samples from adults and nestlings (Thusius et al. 2001b) for each brood of radiotracked pairs, as well as neighbouring pairs. DNA was extracted from blood samples of 64 adults and 234 nestlings using a 5 M NaCl solution (Miller et al. 1988).

Paternity analyses were conducted using four polymorphic microsatellite loci developed for other warbler species (Dawson et al. 1997; Webster et al. 2001). The PCR conditions and thermal cycling profiles follow Thusius et al. (2001b), except in this study we used 0.8 mM dNTPs for all four loci. PCR products and a Genescan 500 fluorescently labelled size standard were run on an automated sequencer (ABI 373; 6% polyacrylamide gel). Allele sizes were determined with Genotyper 2.0 software (Applied Biosystems Inc., Foster City, California, U.S.A.).

We used allele frequencies to calculate the parentage exclusion probability for each locus (P_{Ei}, range = $0.706-0.921$; Jamieson 1994). The combined probability of paternity exclusion (P_{Et}) for all four loci was greater than 0.999. Offspring that matched their putative father at all four loci were considered within-pair young. Offspring that mismatched their putative father at one or more loci were considered extrapair young. For offspring that mismatched at just one locus, we calculated the probability of chance inclusion (Jeffreys et al. 1992) for the three matching loci. In all such cases ($N = 14$), offspring had a high probability of chance inclusion (>0.05; $\overline{X} \pm SE = 0.38 \pm 0.04$; range $0.06-0.69$) and, thus, were considered extrapair young (Johnsen et al. 2000). Means are reported with standard errors and all tests are two tailed. Sample sizes varied because it was not always possible to obtain data from all birds.

RESULTS

Male and Female Extraterritorial Behaviour

During the breeding seasons (May–July) of 2002 and 2003, we tracked 13 pairs for an average of 20.3 ± 3.5 h each (total = 264 h; range $3-42$ h; Table 1). Seven of the

Table 1. Extraterritorial forays and extrapair fertilizations of radiomarked common yellowthroats, 2002–2003

Year	Male/ female	Male mask size (mm²)	Time tracked (h)*	Forays off territory (N)		Mean foray duration (min)		Total territories visited (N)†		Extrapair fertilizations‡
				Male	Female	Male	Female	Male	Female	
2002	ONG/PPE	318§	12	0	0					0/4
	BBR/WOW	277	12	5	2	4	34	2	2	
	BMW/NYA	322	15	3	1	9	18	3	1	2/2
	OEM/BON	259§	15	0	0					0/4
	WOR/MYG	222	3	0	3		35		3	0/1
	OON/BGP**	305	15	0						
	WAY/PRR**	233	19		1		75		1	
2003	NOR/ARY	245	42	0	0					1/4
	RWY/GAB	319	32	1	0	9		1		1/1
	BAR/ABY	442	27	3	0	6		1		
	GEM/YRN	246	6	0	2		14		2	1/4
	BOG/PGY	296	30	3	1	4	15	1	1	0/2
	OON/ANA	355	26	6	3	4	13	4	2	0/4
	ABB/MEA	230	8	1	0	4		1		
	BYR/BEE	357	37	35	0	7		6		1/3

*Time tracked is total time radiotracked simultaneously for the pair or individually for the two females (BGP and PRR in 2002).
†Total territories visited is the sum from all known forays.
‡Number of extrapair young/total number of offspring genotyped.
§Territory was outside the centre of the study area, so it is not shown in Figs 1 and 2.
**Mates of these females were not radiotracked. Their mask sizes are given for reference to Figs 1 and 2.

13 pairs had one member tracked an additional 6.3 ± 1.9 h (total $= 69$ h) because one member of the pair had a battery that failed or individuals were not captured on the same day. In two additional cases, we were unable to capture the male of a pair but continued to track the female throughout her fertile period. Females were tracked for an average of 15.6 ± 2.4 h during their fertile period ($N = 15$ females) and 11.3 ± 3.0 h during incubation (nonfertile period; $N = 8$ females). Most birds either gained or maintained their weight while radiomarked (paired $t_{13} = 0.66$, $P = 0.52$). Birds had full manoeuvreability and were observed routinely foraging in trees and giving elaborate flight song displays.

Both sexes engaged in extraterritorial forays. Eight of 13 (62%) males and seven of 15 (47%) females made extraterritorial forays (Table 1). All of these forays were onto the territories of immediate neighbours (91%, 64 of 70 forays) or one territory further away (9%, 6 of 70 forays; Figs 1, 2). We detected a total of 57 male and 13 female forays (Table 1). All forays occurred between 0510 and 1230 hours, with the majority (87%) occurring between 0600 and 1100 hours. Female forays (29.2 ± 8.4 min) lasted significantly longer than male forays (5.9 ± 0.8 min; independent sample t test: $t_{13} = 3.0$, $P = 0.011$); however, average foray rates for males (0.22 ± 0.10 forays/h) and females (0.14 ± 0.05 forays/h) were similar ($t_{13} = 0.70$, $P = 0.50$). These foray rates were calculated using the total hours of observation during both fertile and nonfertile periods. Foray rates of males (0.12 ± 0.05 forays/h) and females (0.12 ± 0.04 forays/h) were also similar when we compared the foray rates of pairs using just the hours of observation during the fertile period (paired t test: $t_8 = 0.02$, $P = 0.98$; excludes three pairs in which neither bird forayed). Overall, males and females spent 2.3% and 6.1%, respectively, of their time on forays to other territories.

Females only left their territories during their fertile period, and during 54% (7 of 13) of forays we observed the female within 1 m of an extrapair male. Most forays (77%, 10 of 13) were to territories of males with prior breeding experience on the study area; among all males on the study area, 39% (11 of 28) in 2002 and 47% (17 of 36) in 2003 had prior breeding experience. Females visited extrapair males with more prior breeding experience (1.8 years) than their social mate (0.14 years; paired t test: $t_6 = 3.1$, $P = 0.02$). No within-pair or extrapair copulations were observed, however, because females were extremely secretive and all interactions between the female and the extrapair male took place on or near the ground in thick vegetation. During the majority of female forays (85%), the social male either appeared unaware of his mate's absence and showed no obvious response (31%), or he increased his song rate (54%), often from high perches. In two cases the social male followed the female during a foray, and in both cases he was chased away by the extraterritorial male.

Most forays by males were into territories with resident females that were fertile (43 of 57 forays; 75%). However, male forays did not appear to be affected by the fertility status of the male's own mate. Males forayed at a similar rate during their mate's fertile (0.16 ± 0.06 forays/h) and nonfertile (0.23 ± 0.17 forays/h) periods (paired t test: $t_5 = 0.31$, $P = 0.77$; excludes five males that did not foray). One male made 35 forays, all during his mate's nonfertile period. After excluding this male, the foray rate declined during the nonfertile period (0.04 ± 0.05 forays/h), but it was not significantly different from the fertile period (0.19 ± 0.07 forays/h; paired t test: $t_4 = 1.89$, $P = 0.13$).

Males behaved covertly during extraterritorial forays and never sang during an intrusion. We observed the intruding male within 1 m of the resident female during 14 of the 57 (25%) male forays, and, thus, they could have engaged in an extrapair copulation, but it was often difficult to observe the pair continuously during these encounters because they were typically hidden in vegetation near the ground. Birds could also have copulated during
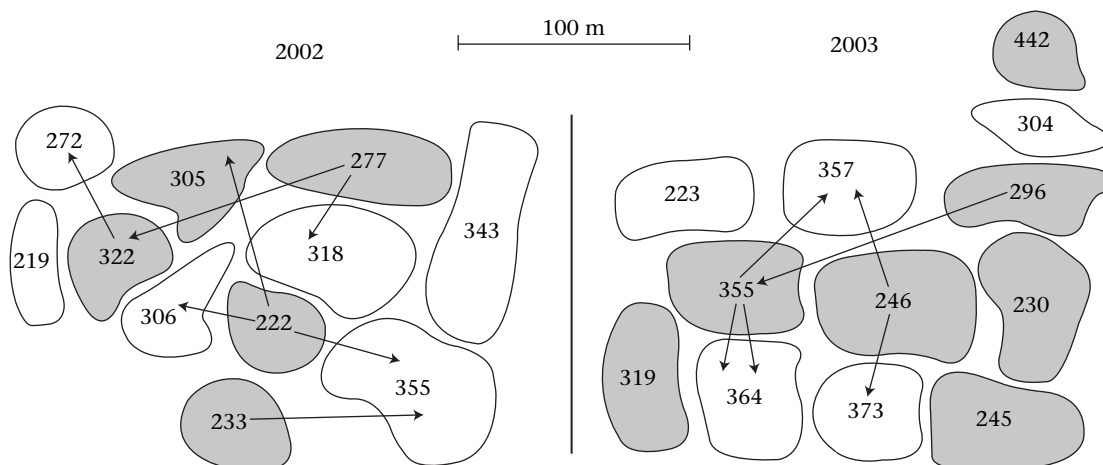

Figure 1. Schematic map of extraterritorial forays by female common yellowthroats, 2002 and 2003. Shading indicates territories of females that were radiotracked. The base of each arrow indicates the territory of a radiomarked bird and the arrowhead indicates the territory that they visited during a foray. Numbers inside each territory represent the total mask size (mm^2) for each male. Note that females PRR and BGP in 2002 were tracked on the territories of their social mates (mask sizes of 233 and 305 mm^2, respectively; see Table 1), but their social mates were not radiotracked. Territories of two additional pairs (see Table 1) were outside the centre of the study area and are not shown.
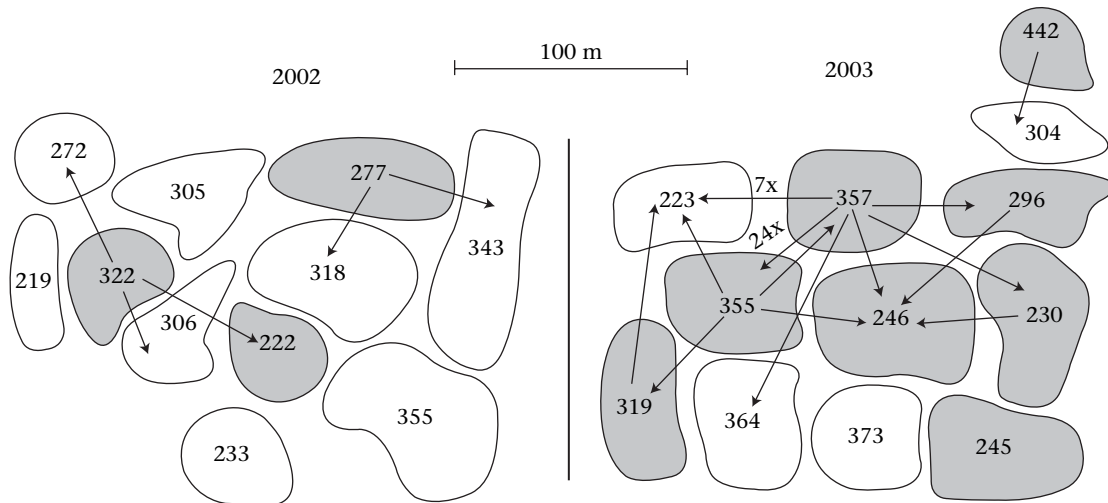
Figure 2. Schematic map of extraterritorial forays ($N = 57$) by male common yellowthroats, 2002 and 2003. Shading indicates territories of birds that were radiotracked. The base of each arrow indicates the territory of a radiomarked bird and the arrowhead indicates the territory that they visited during a foray. Numbers along the arrow indicate multiple forays to the same territory. Numbers inside each territory represent the total mask size (mm²) for each male. See Fig. 1 legend and Table 1 for more details.

the other 43 male forays, but we did not know whether the male came close to the resident female. We found no differences between males that forayed and the males whose territories they entered in terms of breeding experience (chi-square test: $\chi_1^2 = 0.35$, $P = 0.55$). Almost half of male forays (27 of 57; 47%) ended with an aggressive encounter between the resident male and the extraterritorial male.

Extraterritorial Movements and Male Ornaments

Of the seven females that forayed off their territory, six visited territories of males with larger masks than their social mate (binomial test: $P = 0.055$). Four of seven females were observed making more than one foray, but only one female visited the same male twice (Fig. 1). In a paired comparison, females tended to visit extraterritorial males with larger masks (336 ± 13 mm²) than their social mate (279 ± 18 mm²; paired t test: $t_6 = 2.38$, $P = 0.055$; mask sizes were averaged when females visited multiple males; Fig. 1). The other male ornaments did not differ between extraterritorial and social mates (border and bib size and bib colour; all $P \geq 0.18$). The majority of forays (91%) were to immediate neighbours, and two of the seven females that made forays only had neighbouring males with larger masks than their social mate (see territories 222 and 277 in 2002 in Fig. 1). This may have limited female options for mate choice, so we conducted a randomization test to determine whether the observed difference in mask size between social and extraterritorial males ($336 - 279 = 57$ mm²) was greater than expected if females visited their immediate neighbours at random. Although a randomly foraying female would visit neighbours with larger masks than her social mate on average (mean difference $= 24$ mm²), our observed difference in mask size (or one larger) occurred in just 2.25% of simulated random forays ($N = 2000$). Thus,

females observed during radiotracking showed a significant ($P = 0.0225$) bias towards visiting neighbours with relatively larger masks than their social mate. We also compared the mean mask size of males that the female visited with the mean mask size of neighbouring males that she did not visit. Females visited neighbouring males with larger masks (336 ± 12.7 mm²) than the neighbours they did not visit (281 ± 7.8 mm²; paired t test: $t_6 = 3.30$, $P = 0.02$; Fig. 1). Overall, females that forayed were paired with males that had slightly smaller masks (279 ± 18.5 mm²) than the mates of females that did not foray (309 ± 24.3 mm²), but this difference was not significant ($t_{13} = 0.98$, $P = 0.35$).

Of the 13 males radiotracked, eight (62%) intruded onto neighbouring territories (Fig. 2). Males that forayed tended to have larger masks (325 ± 22.3 mm²) than males that did not leave their territories (258 ± 16.0 mm²; $t_{11} = 2.15$, $P = 0.054$). There was no such relationship between other male ornaments and foraying (mask border: $t_{11} = 0.008$, $P = 0.99$; bib size: $t_{11} = 0.04$, $P = 0.97$; bib colour: $t_{11} = 1.18$, $P = 0.26$).

Males directed their extraterritorial forays towards territories of males with smaller masks than their own. Of the eight males that left their territories, seven intruded onto territories of males with the same ($\pm 10\%$) or smaller masks (binomial test: $P = 0.004$). In a paired comparison, intruding males had larger masks (336 ± 12.7 mm²) than the average mask size of all the males whose territories they visited (281 ± 7.8 mm²; paired t test: $t_7 = 2.39$, $P = 0.048$). In a paired comparison of bib colour, we found that males intruded onto the territories of males with more colourful bibs (0.55 ± 0.13) than their own (-0.80 ± 0.44; $t_7 = 2.78$, $P = 0.03$). No such differences were found for border size ($t_7 = 0.45$, $P = 0.67$) or bib size ($t_7 = 0.031$, $P = 0.98$).

We also compared the mask sizes of neighbouring males to determine whether males were visiting neighbours whose masks were relatively smaller than their own.

Indeed, among all neighbouring males, the mask sizes of males whose territories were visited were smaller (274 ± 12.4 mm^2) than those of neighbours whose territories were not visited (334 ± 19.6 mm^2; paired t test: $t_7 = 2.76$, $P = 0.03$). There was no such difference for other male ornaments (mask border: $t_6 = 0.25$, $P = 0.81$; bib size: $t_7 = 1.95$, $P = 0.09$; bib colour: $t_7 = 0.23$, $P = 0.82$).

Extrapair Paternity and Male Ornaments

In this study, 44 of 234 (19%) offspring were the result of extrapair mating in 28 of 63 broods (44%). We were able to assign parentage to 40 of 44 (91%) extrapair offspring, all of which matched the assigned extrapair sire, and no other male, at all four loci. Neighbouring males sired 32 of 40 (80%) extrapair offspring. The remaining extrapair offspring were sired by males residing one (15%) and two (5%) territories away. All offspring matched their putative mother at all four loci.

In a paired comparison, extrapair sires had larger masks (328 ± 8.1 mm^2) than the male that they cuckolded (305 ± 10.3 mm^2; mean difference $= 23$ mm^2; paired t test: $t_{17} = 2.30$, $P = 0.03$). We found no such differences for mask border ($t_{17} = 0.42$, $P = 0.68$), bib size ($t_{16} = 0.69$, $P = 0.50$) or bib colour ($t_{15} = 0.78$, $P = 0.45$). In seven cases, a male cuckolded more than one male, and in these analyses we used the mean ornament size of all males that a particular male cuckolded. There was also no difference in breeding experience between extrapair sires and the males that they cuckolded (chi-square test: $\chi^2_1 = 0.03$, $P = 0.87$).

Extraterritorial Movements and Extrapair Fertilization Success

Five nests failed because of nest predation or desertion after cowbird parasitism, so we were only able to genotype broods of 10 of 15 radiotracked females. We sampled 29 of their offspring, of which six (21%) were extrapair young (Table 1). At three territories (containing four of the six extrapair young), we observed the extrapair sire enter the territory of the female when she was fertile. At another territory, we observed a fertile female enter the territory of the male that sired her one extrapair young. In all of these cases, birds were hidden in thick vegetation and we could not determine whether copulation occurred during that particular visit, but paternity analyses revealed that they copulated at some point. Thus, we know that both males and females seen visiting other territories can gain extrapair fertilizations with the resident bird.

DISCUSSION

Both male and female common yellowthroats forayed off their territories, and the pattern of these forays was associated with both a male ornament (mask size) and potential mating opportunities. Females only forayed during their fertile period and they directed their forays to a limited subset of neighbouring males with larger ornaments. In contrast, males forayed at the same rate during and after their own mate's fertile period, and they directed most of their forays to fertile females on other territories (75%) where the resident male had a smaller ornament. Furthermore, genetic analysis of the broods of radiotracked birds (this study) and larger-scale paternity analyses (Thusius et al. 2001b) revealed that males with larger masks were more likely to gain extrapair fertilizations. To date, no other study has found a male ornamental trait that is linked to both extraterritorial forays and extrapair fertilizations. A handful of studies have linked extraterritorial movements of females to other aspects of male quality, such as body size, age, timing of moult or social rank, but most studies have found no relationship between forays and male quality (Table 2 in Westneat & Stewart 2003; see also Neudorf et al. 1997). Below we argue that extraterritorial forays in common yellowthroats are most likely related to the extrapair mating tactics of each sex, and we discuss the implications of our results for sexual selection on male ornamental traits.

It has been suggested that females might leave their territories to forage for nesting material or food on other territories, rather than to seek extrapair matings (reviewed by Westneat & Stewart 2003). In common yellowthroats, for example, female forays may be restricted to the fertile period because they are searching for nesting material or food, while the absence of forays during incubation (nonfertile period) may simply reflect the time constraints of incubating a clutch. However, forays are relatively uncommon events (1 foray every 7.1 h) that constitute a small percentage (6%) of a female's time, and, thus, it seems unlikely that incubation would completely prevent extraterritorial forays for food. Furthermore, we do not think that these alternative ideas provide as compelling an explanation for why females tended to visit neighbours with relatively smaller masks than their own mate. It may be that males with larger masks also have larger territories or territories with more resources (food or nesting material), but our evidence does not support this view. Mask size is not related to territory size (Thusius et al. 2001b; P. Dunn, unpublished data) and food abundance (estimated from biweekly sweep-net samples of insects) does not vary significantly among territories in the area examined in this study (conifer bog; P. Dunn, unpublished data). Furthermore, we have never seen females gathering nesting material outside of their territories, and many extraterritorial forays (54%) resulted in females approaching a neighbouring male within 1 m, which suggests that females were attempting to approach extraterritorial males on their forays. It is difficult to entirely eliminate alternative functions of extraterritorial forays by females without seeing copulations, but given that the behavioural patterns corroborate the fertilization patterns, we think it is likely that females (and males, see below) participate in forays to gain extrapair matings.

The pattern of forays by male common yellowthroats is more clearly related to extrapair mating tactics. Males that forayed had larger masks than males that did not leave their territories, and they directed their forays towards territories of neighbours that had both smaller masks and fertile mates and, thus, a greater opportunity to gain extrapair paternity (Thusius et al. 2001a; this study).

Controlled experiments in an aviary indicate that males with larger masks are dominant over males with smaller masks (Tarof et al. 2005). The relatively greater dominance of males with larger masks may allow them greater access to extrapair matings on the territories of neighbours with smaller masks. This dominance behaviour may be sufficient to explain the greater extrapair mating success of males with larger masks. However, females also show a strong preference for males with larger masks in aviary experiments (Tarof et al. 2005). Thus, it seems relatively clear that male forays are involved in extrapair mating, either directly by males visiting neighbouring females and gaining extrapair copulations on their territories or by advertising themselves to females that later copulate with the extrapair male on his territory. The role of females is less clear, because the dense vegetation prevented us from seeing copulations, but, as we have argued above, we think it is likely that both sexes use forays to gain extrapair copulations.

Few other studies have made detailed observations of the extraterritorial forays of socially monogamous birds, but even in this small sample there appear to be different patterns. In hooded warblers, *Wilsonia citrina* (Neudorf et al. 1997; Stutchbury 1998) and common yellowthroats, both males and females make extraterritorial forays, but it is not clear whether extrapair fertilizations generally occur during male or female forays, or both. Our limited evidence suggests that either type of foray could result in extrapair fertilizations in common yellowthroats (three males and one female were seen foraying and they successfully gained extrapair fertilizations). On the other hand, in superb fairy-wrens, it appears that extrapair copulations occur primarily during female forays before sunrise (Double & Cockburn 2000). It is important to note that these female forays were only discovered by radiotracking before dawn, and male forays, which are conspicuous and occur throughout the day and year, rarely result in extrapair copulations (Mulder 1997). We specifically looked for pre-dawn forays in common yellowthroats, but did not find any. Another pattern may occur in bluethroats, *Luscinia s. svecica*, as fertile females visit males on other territories (Smiseth & Amundsen 1995), yet extrapair copulations have only been witnessed during male visits to the female (Johnsen et al. 1998). The handful of studies to date illustrate how little we know about how extrapair copulations occur, yet such information is important in light of the claim that extrapair copulations are unlikely to provide females with substantial genetic benefits (Arnqvist & Kirkpatrick 2005).

The participation of both sexes in extraterritorial forays suggests that both female choice and male–male competition are likely to influence extrapair mating. Both of these processes of sexual selection appear to favour males with larger masks in common yellowthroats (see also Tarof et al. 2005). Such reinforcing selection is often expected to produce strong directional selection on male ornaments (Kodric-Brown & Brown 1984; Berglund et al. 1996). However, there are a number of reasons why such selection may be weaker than expected. Our results suggest that one reason may be the spatial distribution of male fertilization success in the population. For a given level of extrapair fertilization in a population, the intensity of sexual selection will vary with the proportion of males that gain those fertilizations. Selection will be relatively strong if only a small proportion of males sire most of the extrapair young and weaker if those fertilizations are shared by many males. For example, in the sand goby, *Pomatoschistus minutus*, cuckoldry actually reduces the intensity of sexual selection because it allows sneaker males to gain fertilizations at the expense of polygynous males, which tend nests containing the clutches of several females (Jones et al. 2001). In this case, sneaking reduces the high skew in male reproductive success caused by polygyny.

We suggest that the foraying behaviour of common yellowthroats may have a similar effect on sexual selection. Forays occurred primarily to immediate neighbours, and most males made forays (62%). Almost half of males (45%) gained extrapair fertilizations (Whittingham & Dunn 2005), and, thus, extrapair fertilizations were gained by many males, rather than being monopolized by a few males. In this case, extrapair fertilizations occurred at a local, rather than global, scale, which is less likely to produce a strong increase in sexual selection (Webster et al. 2001; Whittingham & Dunn 2005). Indeed, most of the variance in male reproductive success was attributable to within-pair (58%), rather than extrapair (21%), components in common yellowthroats (Whittingham & Dunn 2005). Extrapair fertilizations should have a stronger effect on sexual selection when a minority of males gain most of the extrapair fertilizations and foray distances are longer, so copulation partners become available over a larger scale. In some other species, foray distances are relatively longer than in common yellowthroats (Dunn & Whittingham 2005; Woolfenden et al. 2005) and the effect on sexual selection may be very different.

In summary, extraterritorial movements of both male and female common yellowthroats were related to a male ornamental trait (mask size), which was also associated with patterns of extrapair fertilization. Thus, in this species, both male–male competition and female choice appear to contribute to extrapair fertilizations. Further studies of movements by each sex may help to explain how extrapair fertilizations occur and, ultimately, their effect on sexual selection.

References

Arnqvist, G. & Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist, Supplement*, **165**, S26–S37.

Berglund, A., Bisazzo, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–399.

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.

Candolin, U. 2004. Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. *Evolution*, **58**, 1861–1864.

Dawson, R. J. G., Gibbs, H. L. & Yezerinac, S. M. 1997. Isolation of microsatellite DNA markers from a passerine bird, *Dendroica petechia* (the yellow warbler), and their use in population studies. *Heredity*, **79**, 506–512.

Double, M. & Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society of London, Series B*, **267**, 465–470.

Dunn, P. O. & Whittingham, L. A. 2005. Radio-tracking of female tree swallows prior to egg-laying. *Journal of Field Ornithology*, **76**, 259–263.

Forsgren, E. 1997. Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society of London, Series B*, **264**, 1283.

Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.

Guzy, M. J. & Ritchison, G. 1999. Common yellowthroat (*Geothlypis trichas*). In: *The Birds of North America. No. 448* (Ed. by A. Poole & F. Gill. Philadelphia: The Birds of North America.

Hanski, I. K. 1994. Timing of copulations and mate guarding in the chaffinch *Fringilla coelebs*. *Ornis Fennica*, **71**, 17–25.

Jamieson, A. 1994. The effectiveness of using co-dominant polymorphic allelic series for (1) checking pedigrees and (2) distinguishing full-sib pair members. *Animal Genetics*, **25**, 37–44.

Jeffreys, A. J., Allen, M., Hagelberg, E. & Sonnberg, A. 1992. Identification of the skeletal remains of Josef Mengele by DNA analysis. *Forensic Science International*, **56**, 65–76.

Johnsen, A., Lifjeld, J. T., Rohde, P. A., Primmer, C. R. & Ellegren, H. 1998. Sexual conflict over fertilizations: female bluethroats escape male paternity guards. *Behavioral Ecology and Sociobiology*, **43**, 401–408.

Johnsen, A., Andersen, V., Sunding, C. & Lifjeld, J. T. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature*, **406**, 296–298.

Jones, A. G., Walker, D., Kvarnemo, C., Lindstrom, K. & Avise, J. C. 2001. How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 9151–9156.

Kodric-Brown, A. & Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist*, **124**, 309–323.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.

Miller, H. L., Dykes, D. & Polesky, H. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Research*, **16**, 1215.

Mulder, R. A. 1997. Extra-pair courtship displays and other reproductive tactics of superb fairy-wrens. *Australian Journal of Zoology*, **45**, 131–143.

Neff, B. D. 2001. Genetic paternity analysis and breeding success in bluegill sunfish (*Lepomis macrochirus*). *Journal of Heredity*, **92**, 111–119.

Neudorf, D. L., Stutchbury, B. J. M. & Piper, W. H. 1997. Covert extraterritorial behavior of female hooded warblers. *Behavioral Ecology*, **8**, 595–600.

Rappole, J. H. & Tipton, A. R. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, **62**, 335–337.

Smiseth, P. T. & Amundsen, T. 1995. Female bluethroats (*Luscinia s. svecica*) regularly visit territories of extrapair males before egg laying. *Auk*, **112**, 1049–1053.

Stutchbury, B. J. M. 1998. Extra-pair mating effort of male hooded warblers (*Wilsonia citrina*). *Animal Behaviour*, **55**, 553–561.

Tarof, S., Dunn, P. O. & Whittingham, L. A. 2005. Dual functions of a melanin-based ornament in the common yellowthroat. *Proceedings of the Royal Society of London, Series B*, **272**, 1121–1127.

Thusius, K. J., Dunn, P. O., Peterson, K. A. & Whittingham, L. A. 2001a. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. *Behavioral Ecology*, **12**, 633–639.

Thusius, K. J., Peterson, K. A., Dunn, P. O. & Whittingham, L. A. 2001b. Male mask size is correlated with mating success in the common yellowthroat. *Animal Behaviour*, **62**, 435–446.

Venier, L. A., Dunn, P. O., Lifjeld, J. T. & Robertson, R. J. 1993. Behavioural patterns of extra-pair copulations in tree swallows. *Animal Behaviour*, **45**, 412–415.

Webster, M. S., Chuang-Dobbs, H. C. & Holmes, R. T. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. *Behavioral Ecology*, **12**, 439–446.

Webster, M. S., Pruett-Jones, S., Westneat, D. F. & Arnold, S. J. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution*, **49**, 1147–1157.

Westneat, D. F. 2000. A retrospective and prospective look at the role of genetics in mating systems: toward a balanced view of the sexes. In: *Vertebrate Mating Systems* (Ed. by M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 253–306. Singapore: World Scientific.

Westneat, D. F. & Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates and conflict. *Annual Review of Ecology and Systematics*, **34**, 365–396.

Whittingham, L. A. & Dunn, P. O. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. *Behavioral Ecology*, **16**, 138–144.

Wong, B. B. 2004. Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Animal Behaviour*, **67**, 583–590.

Woolfenden, B. E., Stutchbury, B. J. M. & Morton, E. S. 2005. Male Acadian flycatchers, *Empidonax virescens*, obtain extra-pair fertilizations with distant females. *Animal Behaviour*, **69**, 921–929.