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Department of Biological Sciences, University of Wisconsin, Milwaukee

Allocation of Male Parental Care in Relation to Paternity Within and Among Broods of the Common Yellowthroat (*Geothlypis trichas*)

Kara A. Peterson, Kevin J. Thusius, Linda A. Whittingham & Peter O. Dunn

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Abstract

The relationship between male parental care and paternity has been investigated in a number of avian species, but in many cases the influences of confounding factors, such as variation in male and territory quality, were not addressed. These sources of variation can be controlled for by making within-male comparisons between successive broods or within-brood comparisons between groups of fledglings in a divided brood. We studied the relationship between male parental care and paternity in the common yellowthroat (*Geothlypis trichas*) at three levels: between groups of fledglings in divided broods, between first and second broods of the same pair, and among all broods in the population. In this study we proposed three hypotheses: first, males in double-brooded pairs should provide relatively more parental care to broods in which they have higher paternity; secondly, after fledging and brood division, males should provide more care to related offspring; and finally, among all broods in the population, paternity should be related positively to male parental care. Brood division occurred in many of the broods studied; however, broods were not divided according to fledgling size or paternity. Furthermore, within divided broods, males fed within-pair and extra-pair fledglings at similar rates. For sequential broods of the same pair, male feeding rates were not associated with differences in paternity between broods. Among all broods in the population, males did not provide relatively less care to broods containing unrelated young. The lack of a relationship between male parental care and paternity suggests that either males cannot assess their paternity or the costs of reducing male parental care outweigh the benefits.

Corresponding author: Linda A. Whittingham, Department of Biological Sciences, PO Box 413, University of Wisconsin-Milwaukee, Milwaukee, WI 53201, USA. E-mail: whitting@uwm.edu

Introduction

Studies using molecular techniques have revealed that genetic relationships between young and parents do not always reflect social relationships. In birds, copulations between females and extra-pair males often result in broods of mixed paternity in which the social father sires only a proportion, if any, of the young (reviewed in Westneat & Webster 1994). The relatedness between young and their social parents may contribute to variation between the sexes in the extent of parental investment. Parental investment theory predicts that a male will provide less care to broods in which he has low paternity because investment in unrelated young provides no fitness benefits and creates additional costs to the male (Trivers 1972). On the other hand, if a male cannot recognize his genetic descendants, then a reduction in male parental care may reduce the probability of survival for all young in the brood, including his genetic descendants. Attempts to model the relationship between paternity and male parental care have revealed the complexity of predicting a male's parental response when his parentage is reduced (Whittingham et al. 1992; Westneat & Sherman 1993).

The parental-investment response of individual males to extra-pair paternity is dependent upon three main factors: (i) the variability and predictability of paternity among breeding attempts; (ii) the ability of males to assess their paternity; and (iii) the reproductive trade-offs involved in reducing parental care (Whittingham et al. 1992; Westneat & Sherman 1993). These three factors represent a hierarchy of assumptions that yield different predictions about the effect of paternity on male parental care. First, paternity must vary between breeding attempts before individual males are expected to alter their level of parental care. Secondly, males must have reliable cues with which to assess their parentage in order to respond to changes in paternity. Finally, the benefits must outweigh the costs of reducing parental care for such responses to be adaptive. The benefits of reducing parental care may include an increased opportunity for gaining additional mates or extra-pair copulations and increased probability of survival to another breeding attempt (Mauck et al. 1999). The cost of reducing parental care may be a reduced probability of offspring survival (Wolf et al. 1988; Bart & Tornes 1989; Dunn & Hannon 1989; Whittingham & Robertson 1994).

The relationship between male parental care and paternity may also be influenced by confounding factors such as differences in territory or male quality (Kempenaers & Sheldon 1997). In a high-quality territory where food is abundant and individuals may expend less energy to obtain resources, a female may be able to raise an entire brood without male parental assistance. In such a scenario, a male may provide little care if he can invest his energy in alternative activities that result in relatively greater benefits (Emlen & Oring 1977). Male quality can be an additional confounding factor. A low-quality male may not be able to guard his mate effectively from intruding males seeking extra-pair copulations and, as a result, he may have low paternity. Such males may also provide little parental care because of their overall poor quality, not because they are adjusting their parental

effort to their paternity. The relationship between paternity and male parental care can be examined while controlling for such confounding factors by studying a species with multiple broods per season and brood division.

The study of successive broods by the same pair during a breeding season allows for within-male comparisons between successive broods with the same mate on the same territory. By doing so, sources of variation in territory quality and male quality will be negligible relative to variation between all mated pairs in the population. Males may allocate relatively more care to the brood in which paternity is highest in order to maximize fitness benefits and minimize the costs of caring for unrelated young. Brood division is another potential means for males to redirect their parental care when faced with providing care to unrelated young. Brood division occurs when fledglings are divided into two groups and each group is cared for by one adult (reviewed in McLaughlin & Montgomerie 1985). It is possible that a male reduces the costs of caring for extra-pair young by providing care only to the portion of the brood he sired. The study of parental care and parentage within divided broods offers some practical advantages because differences in territory quality or male quality are controlled as comparisons are restricted to members of the same brood on the same territory. We studied the relationship between male parental care and paternity in the common yellowthroat (*Geothlypis trichas*), a species that attempts two successive broods per season and exhibits brood division.

In this study we assumed that males can assess their paternity, paternity varies among broods, and the benefits of reducing parental care outweigh the costs. Based on these assumptions we examined three hypotheses. First, males in double-brooded pairs should provide relatively more parental care to broods in which they have higher paternity; secondly, after fledging and brood division, males should provide more care to related offspring; and finally, among all broods in the population, paternity should be related positively to male parental care.

Methods

The common yellowthroat is a small (10 g), socially monogamous warbler with biparental care. The species breeds in wetland areas of the United States and Canada and winters in the southern U.S. south to Panama (Guzy & Ritchison 1999). The male defends a territory while the female builds a nest, incubates the clutch, and broods the nestlings. Both parents feed the young before and after fledging (Hofslund 1959). Following independence, young disperse from their natal territory and, as consequence, adults in the breeding population are unrelated (only 3% of banded nestlings have returned to the study area).

This study was conducted at the University of Wisconsin-Milwaukee Field Station in Saukville, Wisconsin between May and Aug. 1998 and 1999. Adult and fledgling yellowthroats were captured in mist nets. Males were caught prior to nesting using song playback and females were caught during incubation.

Nestlings were banded and measured at 4–5 d of age, prior to fledging from the nest, which typically occurs at 8 d of age. Each bird was banded with an aluminum US Fish & Wildlife Service band and a unique combination of three coloured bands for individual identification. We measured body mass, tarsus, wing, and tail length of each individual. A blood sample (approximately 50 μl) was obtained from each individual for paternity analysis. As a consequence of nest predation (n = 15 nests) and brood parasitism by brown-headed cowbirds (*Molothrus ater*; n = 2), we were able to sample both paternity and male feeds to nestlings at 32 of the 49 nests. Five of these nests were depredated after we collected blood and conducted feeding watches at the nest (overall predation rate: 20 out of 49, 41% nests). In an additional 12 cases the nest was not located, but fledglings were caught and observed. Overall, a total of 44 broods were sampled for both paternity and male parental care.

In the 12 cases in which young were discovered after fledging, brood size averaged 3.3 young (± 1.0, range 2–5). These young were discovered while begging for food from their parents. Parents carrying food were followed to the location of each fledgling and fledglings were captured by flushing them into mist nets. Afterwards these broods were observed intensively to ensure that all young had been captured. Of all the fledglings that died, half were within-pair and half were extra-pair young. Thus, our results were not likely to be affected by differential mortality between within-pair and extra-pair fledglings. A total of 42 adult males, 48 adult females, 125 nestlings, and 42 fledglings were sampled.

Parental care was measured as the rate at which parents fed nestlings and fledglings (food deliveries per hour, Davies & Hatchwell 1992, Dixon et al. 1994; Whittingham & Dunn 1998). We did not examine the quality or quantity of food brought to the brood during each food delivery, and, thus, parental effort could have varied in the type of prey or the quantity of prey delivered. During the nestling period, feeding rates were recorded on videotape once during the early, middle, and late nestling stages (defined as 3–4, 5–6, and 7–8 d after hatching, respectively). A video-camera was mounted on a camouflaged tripod about 2 m from the nest, first for 1 h without recording to allow parents to habituate to its presence and then for 2 h while recording. Feeding of fledglings and brood division was observed for 1 h on each of 3 d (when fledglings were 16, 18, and 20 d old) for each brood. In some broods each parent fed only a portion of the brood. In these cases of brood division, young were dispersed across the territory (mean territory diameter 45 m) and it required two observers to determine the identities of the young fed by the male. As a result, feeding rates of fledglings by females were not quantified. Prior to starting each fledgling feeding watch, the location and identity of all fledglings in the brood were determined so that all feeds by the male could be counted by the two observers. The average number ± SD of fledglings fed by each male was 1.6 ± 0.4 and ranged from 1 to 3. Feeding watches were conducted between 06:30 and 19:00 h for a total of 280 h. Each brood was observed for an average of 2.76 ± 0.83 h as nestlings and 2.95 ± 0.41 h as fledglings.

Paternity Analyses

Parentage of young was determined by multilocus DNA fingerprinting and microsatellite analysis. Multi-locus fingerprinting was used initially for the 1998 samples. In 1999, microsatellite primers were optimized and used for subsequent paternity analyses. Blood samples were stored in Queen's lysis buffer (Seutin et al. 1991) for 1–3 mos until DNA was extracted using a 5-M salt solution (Miller et al. 1988).

All nestlings sampled in 1998 ($n = 57$) and a portion from 1999 ($n = 15$) were analyzed using multilocus DNA fingerprinting following the techniques described in Dunn et al. (1994). All members of a brood were run in adjacent lanes with putative parents run in lanes flanking the young.

Young were considered to be the direct descendants of their putative parents if they had less than two novel bands, which are DNA fragments in the young that are not found in either parent (Westneat 1990), and a band-sharing coefficient (Wetton et al. 1987) greater than 0.436 with each parent (Fig. 1). Novel bands are expected to arise from mutations at a very low rate, about five of every 1000 bands scored (Jeffreys et al. 1985; Burke & Bruford 1987). Mutations occurred at a rate of 1/980 bands, and the probability of two novel fragments arising from mutation was < 0.0001 (calculated from the Poisson distribution, see Burke & Bruford 1987). Thus, we considered mutation to be the cause of single novel bands in any young and extra-pair paternity to be the cause of two or more novel bands. The mean $\pm$ SD number of bands scored per individual was 16 ± 5.6. The mean background rate of band-sharing among unrelated adults (mated pairs, $n = 26$) was 0.16 ± 0.13, whereas the band-sharing between mothers and their offspring was 0.496 ± 0.06, ($n = 78$). Young were excluded as descendants of their putative parents if their band-sharing fell below the one-tailed 99% confidence interval, which in this case was 0.436 (Fig. 1).

Microsatellite DNA was amplified by polymerase chain reaction using primers developed for yellow warblers (*Dendroica petechia*; Dpu01 and Dpu16; Dawson et al. 1997) and black-throated blue warblers (*Dendroica caerulescens*; Dca24 and Dca28; Webster et al., in press). All nestlings sampled in 1999 ($n = 96$) were analyzed at all four microsatellite loci, whereas all nestlings from 1998 ($n = 57$) were analyzed at one, two, or three loci in addition to DNA fingerprinting to verify the microsatellite analyses.

Polymerase chain reaction conditions and thermal profiles are given for Dpu01; if conditions varied for Dpu16, Dca24 and Dca28 they are provided in parentheses, respectively. Polymerase chain reaction was carried out in a total volume of 20 μl with the following reaction conditions: 30–50 ng DNA, 0.5 pmol (0.1, 0.5, 1.0) each primer, 50 mM KCl, 10 mM Tris-HCl (pH 8.3), 2.5 mM $MgCl_2$ (3.75, 3.0, 2.75), 0.2 mM dNTPs (0.2, 0.15, 0.6), and 0.5 U Taq polymerase. The program began with an initial denaturing step at 94°C for 3 min, followed by 30 cycles at 94°C for 30 s (30, 60, 60), 52°C (57, 44, 48) for 30 s (30, 60, 60) and 72°C for 30 s (30, 45, 45). The program concluded with a final cycle at 72°C for 5 min.

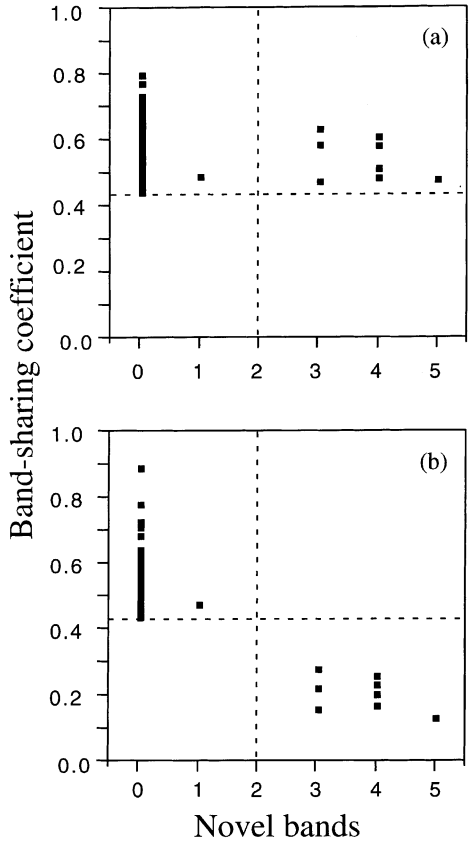

Fig. 1: Criteria for excluding offspring as direct descendants of putative parents on DNA fingerprints. Band-sharing coefficients between offspring and mothers (a) and offspring and putative fathers (b). Young were considered extra-pair if they had two or more novel bands and a band-sharing coefficient less than 0.436 with a putative parent (denoted by stippled lines)

Next, the forward primer was radioactively end-labelled in a reaction containing 0.15 pmol forward primer, 40 mM Tris-HCl (pH 7.6), 10 mM $MgCl_2$, 5 mM DDT, 0.375 U T4 kinase, 0.375 μCi [γ^{33}P]-dATP at 37°C for 30 min. The labelled primer was incorporated into the polymerase chain reaction product in a second polymerase chain reaction which was carried out in a total volume of 10 μl with the following reaction conditions: 30–50 ng of the initial polymerase chain reaction product, 7.5 μmol end-labelled forward primer, 3.0 μmol reverse primer, 50 mM KCl, 10 mM Tris-HCl (pH 8.3), 1.5 mM $MgCl_2$, 2.4 mM dNTPs, and 0.5 U Taq polymerase. The thermal profiles for each locus were the same as above, except that the number of cycles was reduced to 10. Radioactively labelled polymerase chain reaction products were run on a 6% polyacrylamide gel for 4500 V-h at 50°C which was dried, exposed to autoradiograph film, and developed for visualization.

Table 1: Variability of microsatellite loci used for paternity analyses. p_{ei} is the probability of paternal exclusion at an individual locus, h_e is the expected heterozygosity, and h_o is the observed heterozygosity. The total probability of paternal exclusion at all loci (p_{et}) was 0.999

Locus	No. alleles (no. adults)	Mean allele frequency	p_{ei}	h_e	h_o
Dpu01	33(40)	0.03	0.901	0.951	0.85
Dpu16	15(40)	0.07	0.712	0.849	0.85
Dca24	28(40)	0.04	0.868	0.933	0.93
Dca28	21(40)	0.05	0.801	0.899	0.95

Microsatellite allele sizes were determined by reference to a M13 mp18 DNA sequence (Sequenase Version 2.0 DNA Sequencing Kit; United States Biochemical US70770) run on each polyacrylamide gel. Extra-pair young were identified as those that shared an allele with their mother but not with their social father at two or more loci. When an allele at just one of the four microsatellite loci did not match the putative father, the paternity of young was confirmed with multilocus DNA fingerprinting ($n = 15$ young in 1999). The four microsatellite loci used in paternity analyses were highly polymorphic: number of alleles ranged from 15 to 33 and mean allele frequencies ranged from 0.03 to 0.07 (Table 1). The frequency of each microsatellite allele (x_i) was calculated from the total population of adults and then used to calculate the expected frequency of heterozygotes (h_e) as: $h_e = 1 - \Sigma(x_i)^2$. The observed heterozygosities ranged from 0.85 to 0.95 (h_o; Table 1) and were similar to the expected frequencies (Table 1). We calculated the average probability of paternal exclusion (p_{ei}) at each locus (range 0.712–0.901; Table 1). This is the probability that a randomly chosen male will not share the paternal allele found in the young, given that the maternal allele is known (Jamieson 1994). For all four loci the total probability of exclusion was 0.999. We also calculated the probability of chance inclusion for each excluded nestling, which is based on the frequency of each allele in the population (Jeffreys et al. 1992). The mean ± SD of these probabilities was 0.00298 ± 0.00347 ($n = 31$, range 2.0×10^{-4}–1.17×10^{-2}). Thus, the probability that we would not detect extra-pair paternity when it occurred was very low.

Statistical Analyses

The relationship between paternal care and paternity was examined separately for nestlings and fledglings in three ways: (i) between groups within divided broods of fledglings; (ii) between first and second broods; and (iii) across the population. Paternity (proportion of young sired) was arcsine transformed to normalize the data. At the population level, the number of observation periods per nest varied (1–3) as a consequence of nest predation, and this necessitated using a repeated-measures analysis of variance that could tolerate missing values

(MIXED procedure in SAS; Littell et al. 1996). We examined paternal care to sequential broods of the same male which controls for male effects. In the analysis of divided broods of fledglings, we examined paternal care to particular young within a brood, which controls for brood effects. In both of these analyses we used the residuals from the regression of male feeding rate on year, time of season, time of day, brood size, and age of young, where they were significant predictors (estimated separately for nestling and fledgling data sets). Differences in residual male feeding rates and paternity in double-brooded pairs were analyzed with a one-way ANOVA. Power analyses followed methods in Zar (1999). Means ± SD are presented; all tests were two-tailed and the significance level was 0.05.

Results

Over both years, 21 out of 46 (45.7%) broods contained extra-pair young and 31 out of 153 (20.3%) young were sired by extra-pair males. These data include two broods which were sampled only for paternity (no parental care observations). The frequency of broods with at least one extra-pair young was greater in 1999 (17 out of 28 broods, 60.7%) than in 1998 (four out of 18 broods, 22.2%; $\chi^2 = 6.83$, df = 1, $p = 0.01$). The proportion of extra-pair young per nest also tended to be greater in 1999 (25.2%) than in 1998 (13.9%; Mann–Whitney $U = 332.5$, $n_1 = 18$, $n_2 = 28$, $p = 0.08$). In 1998, seven out of 57 (12.3%) young were sired by extra-pair males, whereas, 24 out of 96 (25%) young were sired by extra-pair males in 1999. We found no cases of intraspecific brood parasitism.

All Broods

Overall, males fed nestlings (4.2 ± 1.4 feeds/h) at a lower rate than fledglings (15.8 ± 7.4 feeds/h; $t = 7.1$, df = 40, $p < 0.001$). Male feeding rates to nestlings and fledglings were analyzed separately in relation to year, paternity, time of season (biweekly periods), time of day (three periods), brood size, and age of young using a mixed model analysis (Table 2). Male feeding rate to nestlings was not related to paternity ($p = 0.06$, $n = 32$ nests, Table 2); note that the slope of this relationship was negative (slope = −1.0) rather than positive, contrary to prediction. Males provided more feeds to nestlings as they grew older ($p < 0.01$) and to young that hatched later in the season ($p < 0.01$).

Similarly, paternity did not influence male feeding rate to fledglings ($p = 0.72$, $n = 33$ broods, Table 2), and, again, the slope of this relationship was negative (slope = −1.3). Males provided more feeds to fledglings as they grew older ($p < 0.01$), and they fed fledglings at higher rates in 1999 than in 1998 ($p = 0.04$; Table 2). In separate analyses, we found no relationship between male feeding rate to nestlings ($r^2 = 0.026$, $F_{1,92} = 2.43$, $p = 0.12$) or fledglings ($r^2 = 0.005$, $F_{1,106} = 0.56$, $p = 0.46$) and the opportunities for extra-pair matings, measured as the number of fertile females in the population on the day male parental care was observed.

Table 2: Variables predicting male feeding rate in a mixed model analysis of variance. Shown are full models with all variables likely to influence male feeding rate. Results were similar using reduced models that included only significant variables from the full model and paternity

Independent variable	Nestlings			Fledglings		
	F	df	p	F	df	p
Year	1.2	1,29	0.29	4.7	1,31	0.04
Paternity	11.2	1,29	0.06	0.1	1,31	0.72
Time of season[a]	5.8	4,51	< 0.01	0.5	4,53	0.77
Time of day[b]	1.1	2,51	0.36	0.4	2,53	0.67
Brood size	0.2	1,51	0.66	1.0	1,53	0.31
Age of young	11.2	1,51	< 0.01	9.4	1,53	< 0.01

[a] Five biweekly periods from 9 June to 17 Aug.
[b] Three time categories (4 h each) from 06:00 to 18:00 h.

Divided Broods

A total of 18 broods had sufficient data for analysis of brood division. Broods were excluded from analysis when: (i) expected values were < 5 in the χ^2-test (Zar 1999), which occurred when few feeding visits were observed; (ii) a parent or fledgling was not seen during any observation period; or (iii) predation of the brood occurred prior to 16 d of age. Of the 18 broods analyzed, 13 (72.2%) showed stable brood division in which each fledgling was fed predominantly (78–93% of feeds) or exclusively by one parent and the male fed fledglings in a non-random manner (Table 3). Although female feeding rate to fledglings was not recorded, the identities of young being fed by the female were established to determine whether both parents fed the same fledgling. In two out of 18 broods (11.1%) brood division was unstable (Table 3); these were broods in which each parent fed a subset of young during an observation period (i.e. there was brood division), but the subset of young fed by each parent varied between observation periods (i.e. parents switched from feeding one group of fledglings to another between observation periods). Finally, in three cases (16.7%), there was no brood division (Table 3). These broods each contained only two fledglings, both of which were fed exclusively by the male. The females of these broods either built a second nest ($n = 1$) or left the territory at the end of the breeding season ($n = 2$). Overall, males cared for significantly more fledglings than females: 45 out of 77 fledglings (58.4%) were fed by the male only, 21 (27.3%) by the female alone, and 11 (14.3%) were fed by both parents ($\chi^2 = 23.8$, $df = 2$, $p < 0.001$).

Brood division was not related to paternity. There were five broods with both within-pair and extra-pair young among the 13 cases of stable brood division (Table 3). Males at three of these five broods fed both extra-pair and within-pair young, which was not different from chance (binomial test, $p = 0.31$). Within these five broods, males did not feed within-pair young (10.7 ± 3.9 feeds/h) at a higher rate than extra-pair young (4.2 ± 4.3 feeds/h; paired t-test: $t = 2.3$, $df = 4$,

Table 3: Number of food deliveries to individual yellowthroat fledglings (A–E) in 18 broods. Numbers in bold are male feeds to extra-pair fledglings. Brood division is designated as stable, unstable, or not divided; see text for more details. Broods listed twice were sampled in different years (except for ONG). The one-way χ^2 tests for randomness of feeding by the male. *$p < 0.01$, **$p < 0.001$

Brood Division	Male	Female	Male feeds to: A	B	C	D	E	χ^2 test
Stable	MYM	GWN	39	27	0	0	0	105.0**
	NEW	GAY	25	0	0	0		75.0**
	YNR	ROSE	29	13	0	**0**		54.2**
	OBW	WNY	51	48	**0**			49.6**
	ONG	WEB	42	37	0			40.0**
	RR	BOR	25	**4**	**0**			37.3**
	GEE	BWW	24	5	0			33.2**
	ARE	EBE	34	**19**	**0**			32.9**
	WBB	MEG	**27**	24	7			12.9*
	WOW	MAM	39	0				39.0**
	ORB	OBA	13	2				8.1*
	ORB	OBA	28	2				22.5**
	RYB	YGA	**42**	**10**				19.7**
Unstable	WAM	PAM	13	12	8			1.3
	MYO	PGY	**27**	18				1.8
Not divided	WOW	UB	37	30				0.7
	GYM	MGY	28	**26**				0.1
	ONG	WEB	38	35				0.1

$p = 0.08$), although the power of this test was moderate (power = 0.68). Note that in another seven cases of stable brood division, brood division occurred even though males had only within-pair young in their brood (Table 3). Similarly, in the remaining brood which contained all extra-pair young, the male provided more care to one of the two young. These examples suggest that factors other than paternity influence brood division, because male parental care was distributed non-randomly among young, even in broods composed entirely of young sired by the care-giving male. We found no evidence that broods were divided according to size of young, as estimated by wing chord, tarsus length, or body mass measured during the nestling stage (using residuals corrected for nestling age, paired t-test: $t = -0.09$, $df = 7$, $p = 0.93$). Furthermore, there were no differences in wing chord, tarsus length, or body mass between within-pair and extra-pair young within the same broods (paired t-tests: all $p > 0.10$). Thus, males could not discriminate within-pair and extra-pair young based on size.

Sequential Broods

Twelve pairs were double-brooded within the same breeding season. Paternity varied between broods in seven pairs, but the direction of change

between broods was not predictable. Paternity increased between broods in two cases, decreased in six cases, and did not change in four cases ($\chi^2 = 2.0$, df = 2, $p > 0.25$). Among these males there was no relationship between male parental care and paternity when we compared the difference in male feeding rates between first and second broods with the difference in paternity between broods ($r^2 = 0.14$, $F_{1,10} = 1.57$, $p = 0.24$). In this analysis we only compared feeds to nestlings in one nest with feeds to nestlings in a second nest, and similarly for fledglings; nestling feeding rates were not compared to fledgling feeding rates for the same male. We also used residual feeding rates in this analysis, which controlled for brood size and a variety of other effects (see Methods). Lastly, there was no relationship between male parental care to the first brood and paternity in the second brood ($r^2 = 0.15$, $F_{1,4} = 0.73$, $p = 0.44$).

Discussion

In contrast to some other recent studies of double-brooded species (Dixon et al. 1994; Møller & Tegelström 1997), male parental care was not related to paternity in common yellowthroats. We examined patterns of male parental care at three levels. First, within divided broods, males did not care preferentially for within-pair fledglings, nor did they feed within-pair fledglings at higher rates than extra-pair fledglings. This result is similar to two other studies that have found broods are not divided according to paternity (Burke et al. 1989; Anthonisen et al. 1997). Secondly, between broods of the same pair, differences in male feeding rates were not associated with differences in paternity between broods. This result contrasts with the results of two other studies in which males did adjust feeding rates to changes in paternity between first and second broods (Dixon et al. 1994; Møller & Tegelström 1997). Finally, among all broods in the population, males did not decrease feeding rates to broods containing unrelated young. This result is consistent with studies of most other socially monogamous birds (Whittingham & Dunn, in press).

Brood division is common in birds and occurs in a diverse assemblage of species (McLaughlin & Montgomerie 1985). One of the possible benefits of dividing broods according to paternity is that a male may be able to focus his parental care on the portion of the brood that he sired. Mixed paternity and brood division were common in yellowthroats; however, we found that broods were not divided according to parentage and males did not preferentially feed within-pair young (Table 3). Overall, male parental care was distributed non-randomly among young, even in broods composed entirely of within-pair or extra-pair young, suggesting that factors other than paternity influence brood division.

Although the benefits of brood division were not related to paternity, brood division may be advantageous in yellowthroats if it reduces the loss of young to predators. For example, when the brood is divided into two groups the risk of predation on the entire brood may be reduced. The risk of predation is great for species like yellowthroats (41% of nests and 22% of fledglings were depredated

in our study population) and this may favour both an early age at fledging (8 d of age in yellowthroats) and brood division (McLaughlin & Montgomerie 1985).

In some species, broods are divided according to age (Tuck 1972), size (Slagsvold 1997), or sex (Harper 1985; Byle 1990). It seems unlikely that yellowthroat broods were divided by age because hatching and fledging occurred synchronously within each brood. Nor were yellowthroat broods divided according to size of young. A comparison of three morphological characters (tarsus length, wing chord, and body mass) revealed no differences between groups of young that the male did and did not feed. It is unknown whether yellowthroat broods were divided by sex because sexually dimorphic plumage traits were not yet developed when fledglings were observed.

In two previous studies of double-brooded species, males provided relatively less care to broods containing relatively more extra-pair young (Dixon et al. 1994; Møller & Tegelström 1997). In barn swallows (*Hirundo rustica*), paternity was highly repeatable between broods and female participation in extra-pair copulations reflected the level of extra-pair paternity in the brood (Møller & Tegelström 1997). These copulations could have provided cues to males about their paternity in a given brood. In contrast, paternity varied unpredictably between first and second broods in reed buntings (*Emberiza schoeniclus*) and, although extra-pair fertilization rates were high, no cues were identified that may have provided males with an accurate assessment of their paternity (Dixon et al. 1994). In the current study, which had similar sample sizes to those used in the study by Dixon et al. (1994), paternity also varied unpredictably between successive broods of mated pairs, but male feeding rates to nestlings and fledglings were not adjusted relative to the paternity of the brood as a whole. Although there was a tendency ($p = 0.08$) for males to feed their within-pair young at a greater rate than the extra-pair young within broods, the overall pattern of brood division was not related to paternity (Table 3).

Whether considering divided broods, sequential broods or all broods, a positive relationship between male parental care and paternity is predicted only when two critical assumptions are fulfilled. First, males must be able to accurately assess their paternity. Mate guarding or mating access is a reliable paternity cue in other avian species (Davies & Hatchwell 1992; Whittingham & Dunn 1998). The covert behaviour of female yellowthroats may make it challenging for males to guard their mates and to observe copulations between their mate and extra-pair males. In our study, extra-pair copulations were never observed, even though extra-pair fertilizations were common (46% of broods). The absence of such cues could account for the lack of relationship between male parental care and paternity in common yellowthroats. Secondly, when paternity declines, the benefits of reducing care must outweigh the costs. Males that reduce their care may incur a cost from reduced survival of their own young. In the current study, males always sired at least one young in the nest, and, thus, reducing care may risk the survival of these related offspring. Alternatively, if males are reducing care to seek extra-pair copulations, then we might expect them to provide less care when the opportunities for extra-pair mating are greatest; however, we found no

relationship between male parental care and the number of fertile females on the study area each day. In most species of monogamous birds these two criteria do not appear to be satisfied, which may explain why most male birds do not adjust their level of parental care to paternity (reviewed in Whittingham & Dunn, in press).

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