

Cuckoldry and lack of parentage-dependent paternal care in yellow warblers: a cost–benefit approach

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Abstract. Theory suggests that a male strategy of reducing parental care in response to reduced parentage should evolve only under certain conditions. Expected paternity in subsequent matings is predicted to be primary in effect, because it determines whether there is a future benefit to compensate males for the cost of reduced care. This study, tested whether provisioning of nestlings by socially monogamous male yellow warblers, *Dendroica petechia*, varied with the males' parentage in the brood and how males' paternity varied in subsequent matings. Analysis included observations of parental care from 40 nests (31 of which had paternity determined by multi-locus DNA fingerprinting) and paternity results from 130 families over 3 years. Male care was variable but unrelated to parentage, and males were observed to provide typical amounts of parental care to broods in which they had no parentage. Individual males' within-pair parentage generally declined within a season (with re-nesting), varied inconsistently between years and was unrelated to age or breeding experience. Survival between breeding seasons was low (30%) and independent of within-pair parentage. These patterns collectively suggest that the benefit of facultatively reducing parental care when parentage is reduced rarely exceeds the costs. Thus, selection for parentage-dependent care is apparently absent or weak, which could explain the absence of parentage-dependent care in this population of yellow warblers.

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Some males of biparental species are faced with caring for young to which they may be unrelated, because their mate has copulated with other males and the brood consists partly or entirely of young of extra-pair paternity. Natural selection should favour males that avoid providing costly care to unrelated young, so variation in parentage (the proportion of the young sired) has frequently been proposed as the explanation for intra-specific variation in male parental care (Trivers 1972; Winkler 1987; Montgomerie & Weatherhead 1988). Indeed, some empirical evidence supports this straightforward explanation (e.g. Hatchwell &

Davies 1990, 1992a, b; Dixon et al. 1994; Møller 1994; Weatherhead et al. 1994).

Theoretical models suggest that reduced parentage need not always result in reduced parental care, because the selective value of withholding parental care also depends upon the potential benefit of diverting this investment elsewhere (Dawkins & Carlisle 1976; Maynard Smith 1977, 1982). Thus, if prospects for parentage are worse in the future, then the cost of caring for some offspring in the current brood that are not genetically related will be less than the benefit of withholding care in anticipation of future broods, and a male should give full care to the current brood (Maynard Smith 1977, 1982). Conversely, a male would benefit by reducing care to his current brood when his parentage is reduced if (1) parentage increases in subsequent matings or at least varies randomly between breeding attempts (Xia 1992), or (2) providing less care permits paternity gains through extra-pair mating (Westneat &

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Sherman 1993), because in these circumstances the benefit of withholding care can exceed the costs. Thus, the issue of how parentage influences parental care is a specific form of the more general question of the extent to which parental care is shaped by the trade-off between benefits to current offspring and the costs to parents of reducing their production of future offspring (Clutton-Brock 1991; Westneat & Sherman 1993; Houston 1995).

Models of the effect of parentage on parental care have used various assumptions and therefore have sometimes made conflicting predictions (Westneat & Sherman 1993; Houston 1995). When only the most basic assumptions are fixed, however (i.e. care benefits survival of young and it costs parents in terms of mating effort and/or self maintenance), and other conditions are allowed to vary (e.g. the shape of cost-benefit curves, patterns of paternity in successive matings), these conflicts are reconciled. The effect of parentage on intraspecific variation in parental care is seen to depend upon conditions that are likely to vary between taxa (Westneat & Sherman 1993; Houston 1995).

First, the variability and predictability of paternity in subsequent matings determines whether there is a selective advantage from reducing care in a current breeding attempt in expectation of greater benefits from alternative or future breeding opportunities (Maynard Smith 1982; Xia 1992; Westneat & Sherman 1993). Second, the reliability with which individuals can assess their current parentage determines whether they can respond facultatively to changes in paternity between breeding attempts, or whether selection is constrained to adjust patterns of male care over evolutionary time (Westneat & Sherman 1993). Finally, even when the first two conditions favour parentage-dependent reductions in parental care, this response may be constrained by the unavoidable detrimental effect on kin (Whittingham et al. 1992; Westneat & Sherman 1993), which might occur, for example, when a male cannot distinguish kin from non-kin in a brood that must share his care (e.g. Burke et al. 1989; Lifjeld et al. 1992). These three major conditions influencing the relationship form a hierarchy of influence in their evolutionary effects, because each depends on those previous. For example, invoking the third factor as an explanation for the absence of parentage-dependent

care would be unnecessary if factors 1 and/or 2 could be shown not to favour parentage-dependent care.

In this field study of the yellow warbler, *Dendroica petechia*, our first goal was to determine the relation between parentage and paternal care. We observed parental provisioning of nestlings and used DNA fingerprinting to measure parentage. Results of several studies have shown that male parental care varies with parentage (see above), but others have shown no relationship (e.g. Whittingham et al. 1993; Westneat 1995; Whittingham & Lifjeld 1995). Few investigators have empirically considered the three conditions outlined above as explanations for the relationship between paternity variation and parental care among wild animals (but see Davies 1992; Westneat 1995). Thus, our second goal in this study was to test whether the observed relation between paternity and parental care was consistent with the predicted relation between present versus future reproductive opportunities. We gathered paternity data over three breeding seasons and experimentally manipulated nesting in two breeding seasons to examine paternity in repeated breeding attempts by the same males, both within and between years.

STUDY SPECIES

The yellow warbler is a small (10 g), migratory bird common throughout most of North America, where its basic breeding biology has been extensively studied (e.g. Schrantz 1943; Studd & Robertson 1985, 1988, 1989; Hébert & Sealy 1993; Briskie, in press). Yellow warblers practice biparental care. Both parents feed nestlings and fledglings, both vocalize and approach predators that are near offspring, but only females incubate and brood the young. On average, males feed nestlings more often than do females (Biermann & Sealy 1982; Briskie, in press); among males, however, this contribution to parental care can vary substantially (Studd & Robertson 1985, 1988). Although yellow warblers are socially monogamous and single-brooded, many aspects of their breeding biology suggest that extra-pair fertilizations are widespread; using DNA fingerprinting, we have found extra-pair paternity to be common (Yezerinac et al. 1995).

METHODS

Study Population

We studied yellow warblers breeding in the vicinity of the Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34'N, 76°20'W). Unique colour banding of individuals was begun in 1991 and breeding behaviour was studied from May to July of 1992, 1993 and 1994. Detailed descriptions of field methods, DNA fingerprinting protocols and evaluation of parentage are given in Yezerinac et al. (1995) and are summarized here along with details relevant to this study.

Breeding activity was monitored at three study areas (ranging from 3 to 20 ha) within 10 km of one another. At each site, most males were caught, colour-banded, weighed and measured prior to nest initiation, and most females were captured during incubation. Nests were found by observing females building, by intensively searching vegetation every 2–3 days throughout the breeding season and, for well concealed nests, by following the parents as they fed nestlings. We checked nests every 2–4 days to record, wherever possible, date of clutch initiation, clutch size, hatch date and fledging success.

Parental Care

Observations of parental care behaviour of males and females were made in 1992 using portable video cameras concealed in vegetation 2–5 m from nests. We planned one 2-h observation during each of the early, middle and late nestling stages (defined as 1–3, 4–6 and 7–9 days after hatch, respectively). Because of inclement weather, synchronous breeding and predation, however, the number of nests eligible for observation did not always match the number of video-cameras available. Observation periods averaged longer than 2 h (median=129 min), there were fewer observations of late-stage nestlings, and sets of observations were occasionally made for the same nest on successive days and/or during the same nestling stage. We made 182 h of observations at 40 nests from 4 June to 2 July 1992 between 0636 and 1844 hours EST (median=1045 hours). Parentage was determined for offspring in 31 of these families.

Patterns of Paternity

The pattern of parentage in successive breeding attempts is important in determining whether males will benefit from providing paternity-dependent care. To estimate changes in parentage experienced by males, we sought to measure individual males' parentage in multiple nesting attempts with the same female in a single breeding season and in successive breeding seasons with different mates. Although pairs raise no more than one brood to independence per year, partners remain together following predation of eggs or nestlings and will re-nest three or four times in the same breeding season (S. M. Yezerinac, unpublished data). Nest predation and re-nesting was frequent in the population, enabling us to measure paternity in successive breeding attempts of the same pair by mimicking predation ourselves. Thus, in 1993 and 1994, we collected eggs from some nests (under permit from Canadian Wildlife Service) after 6–7 days of the normal 9–10 days of incubation, using the embryos as a source of DNA, and then sampled offspring from the re-nest(s). We estimated age-related changes in parentage by following banded males over the four years of the study.

DNA Fingerprinting

Blood or tissue samples collected from adults and offspring were used for multi-locus DNA fingerprinting. Briefly, 5 µg of DNA from each individual was digested with the restriction enzyme *Alu* I. The DNA fragments were separated according to size in an agarose gel, transferred by Southern blotting onto Immobilon (Millipore) membranes and hybridized with radioactively labelled *Per* and 33.15 probes (Jeffreys et al. 1985; Shin et al. 1985). The presence of bands not found in either social parent (novel genetic markers) and band-sharing coefficients (Wetton et al. 1987) were used to establish parentage. We concluded that adults with ≥ 6 novel bands and/or band-sharing values ≤ 0.40 were not the parents of offspring. These two criteria were never in contradiction. In 39 of the 130 (30%) families analysed, a DNA sample was not available from the female. In the 91 families where the female was fingerprinted, there was no intraspecific brood parasitism; the mismatched parent was always the putative father. Thus, when only the male was

Table I. Relationships between male and female feeding rates and age of nestlings and number of nestlings

Dependent variable	Independent variable	$F_{1,77}$	b	P
Male feeding rate	Number	2.97	0.44	0.084
	Age	40.20	0.745	<0.001
Female feeding rate	Number	2.99	0.37	0.084
	Age	11.24	0.33	0.001

The overall multiple regression is significant in both instances ($F_{2,77} \geq 8.78$, $r^2 \geq 0.19$, $P \leq 0.001$).

sampled, low band sharing with offspring was taken as evidence of extra-pair paternity. Many extra-pair-sired offspring had their true father identified; extra-pair sires' had band-sharing coefficients ≥ 0.40 with offspring and their genotypes accounted for all novel bands (Yezerinac et al. 1995).

Data Analysis

Not all the nests we observed were matched for nestling age or the number of nestlings. To control for these potential sources of variation in parental provisioning rates in comparisons among parents we took residuals from multiple regressions (done separately for males and females), relating feeding rate to age (days since hatch of first nestling) and number of nestlings (Table I). For these regressions, we treated all observation sessions as independent data points. Although allowing multiple observations of the same parent to serve as independent data points is strictly incorrect (Machlis et al. 1985), it permitted us to take residual values for all observations from a common regression. The pseudoreplication did not influence which factors were significant, nor did it systematically bias the residual scores. We checked for these potential effects by running an identical ANOVA model 25 times, each time randomly selecting, with replacement, one datum (observation session) for each nest. Average F statistics across the replicates were significant ($P < 0.05$) for all the same effects, and residual scores from the partial data sets were strongly correlated with residuals from the full data set (mean r for the regressions was ≥ 0.976). To avoid pseudoreplication in subsequent analyses using these residuals, we used either the mean residual score for all observations of the same

parent(s) or employed repeated measures ANOVA models.

Many nests were found after clutch initiation. Thus, we calculated nest success and made comparisons of success among different groups using the Mayfield (1961, 1975) method. All statistical analyses were done using JMP Version 3 (SAS Institute, Cary, North Carolina) and Statview SE+ Graphics v1.04 (Abacus Concepts, Berkeley, California).

RESULTS

Parental Care

Both parents fed the offspring in all but one observation period. Older nestlings were fed more frequently by both parents and relatively more by the male (Fig. 1). Among both males and females, there was variation in the frequency of feeding nestlings of the same ages. This variation in feeding rate (using residuals; Table I) was not

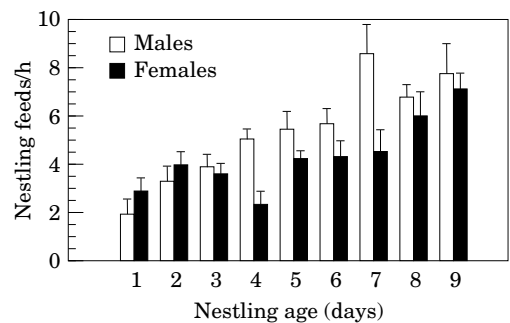


Figure 1. The mean \pm SE number of feeding trips made by males and females to nests at different nestling ages. Number of pairs observed at ages 1–9 days are 6, 12, 12, 7, 13, 9, 11, 6 and 3, respectively.

associated with either diurnal or seasonal variation in time of observation; relative feeding rates did not vary significantly with time of day (observations grouped into quartiles (0714–0832 hours; 0833–1044 hours, 1045–1321 hours, 1322–1740 hours) of $N=20$ using the midpoints) for either males ($F_{3,76}=0.24$, $P=0.87$) or females ($F_{3,76}=2.21$, $P=0.09$); there were no consistent differences in feeding rates between early, mid or late-season observations (day of year, 156–164, $N=30$; 165–169, $N=26$; 170–184, $N=24$) for either males ($F_{2,27}=1.75$, $P=0.18$) or females ($F_{2,27}=2.38$, $P=0.10$). The proportion of total feeds to nestlings provided by the male was unrelated to the time of day ($F_{3,37}=2.19$, $P=0.10$) or seasonal category ($F_{2,78}=2.31$, $P=0.11$). Consistent differences in parental care were evident among parents. Nested ANOVAs showed that 27.6% of variation in relative male feeding rate (using residuals) and 19.9% of variation in relative female feeding rate occurred between individuals, with the remainder occurring between repeated observations of the same individual. Similarly, 32.8% of variation in the proportion of feeds provided by the male occurred between pairs.

Differences in nestling provisioning rates were not associated with differences among males in parentage. Males that had lost paternity did not provision nestlings at relatively lower rates than males with full parentage (mean \pm SE of relative feeding scores: full paternity = -0.12 ± 0.17 , $N=12$; reduced paternity = 0.11 ± 0.14 , $N=19$; $F_{1,29}=1.11$, $P=0.30$). Similarly, the proportion of total feeds that males provided to nestlings did not differ between males depending upon their parentage (full paternity 0.56 ± 0.03 , $N=12$; reduced paternity 0.55 ± 0.04 , $N=19$; $F_{1,29}=0.02$, $P=0.90$). Our sample of nest observations was biased towards younger nestlings for reasons outlined above, which would have made it more difficult to detect a relationship between paternal care and parentage if it were manifested when nestlings were older, feeding rates were higher and the cost to parents was greatest. In each of these analyses, however, there was no effect of nestling age on the difference in feeding rates between males with full and reduced parentage, and the non-significant difference in feeding rates between cuckolded and uncuckolded males was actually opposite to this prediction. Age-main effect and its interactions were non-significant ($P>0.05$) in the previous two models and, inter-

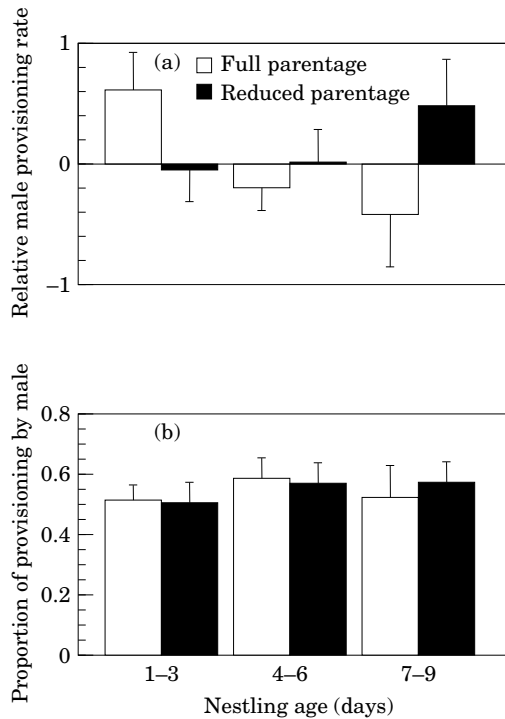


Figure 2. Mean \pm SE relative provisioning rates after removing variation due to age and number of nestlings for males with full paternity (white bars) and males with reduced paternity (black bars). (b) Proportion of total feeds given by males with full paternity and males with reduced paternity.

actions were removed from final calculations (Fig. 2).

There was no evidence of a parentage threshold effect on male parental care. Males with full paternity, partial paternity and no paternity did not differ significantly in either relative feeding rates (full paternity = -0.12 ± 0.17 , $N=12$; partial paternity = -0.02 ± 0.21 , $N=16$; no paternity = 0.91 ± 0.50 , $N=3$; Kruskal–Wallis ANOVA chi-squared approximation; $\chi^2=1.91$, $df=2$, $P=0.38$) or in the proportion of total feeds they provided to nestlings (full paternity = 0.56 ± 0.03 , $N=12$; partial paternity = 0.51 ± 0.04 , $N=16$; no paternity = 0.69 ± 0.06 , $N=3$; Kruskal–Wallis $\chi^2=1.92$, $df=2$, $P=0.38$). Although the power of these tests to detect a difference was low, even the distribution of values failed to suggest a difference. Two of the three males with no paternity in the brood were among the top five males in the sample for provisioning measures.

Table II. Paternity in successive nests of the same male–female pair within the same breeding season

Re-nest	Initial nest		
	No extra-pair paternity	Extra-pair paternity	
No extra-pair paternity	10	Higher	1 Lower
Extra-pair paternity	7	7	3 Same 2

Proportion of young due to extra-pair paternity in the re-nest is expressed as higher, lower or the same level as in the previous nest.

Parental Care and Nest Success

The presumed cost of reduced parental care is reduced nest success. Although there was variation in parental provisioning to nestlings and in nest success, the two did not co-vary strongly in this sample. The mean relative feeding rate (male+female feeding rate, controlling for age and number of nestlings) was not significantly related to the proportion of hatched young that ultimately fledged, either in the complete sample ($r_s=0.23$, $N=40$, $P=0.15$) or among just those nests that were not depredated and therefore fledged young ($r_s=-0.07$, $N=24$, $P=0.73$). Relative male and female feeding rates were not significantly related ($r_s=-0.13$, $N=40$, $P=0.43$). Relative female provisioning rate, relative male provisioning rate and proportion of feeds by males were each unrelated to the proportion of hatched young that ultimately fledged, either in the complete sample ($r_s \leq 0.21$, $N=40$, $P \geq 0.20$) or among just those nests that were not depredated and therefore fledged young ($r_s \leq 0.14$, $N=24$, $P \geq 0.50$), although all the correlations were positive. Thus, the variation seen in parental provisioning of nestlings was apparently inconsequential with respect to nest success.

Patterns of Paternity

Over the three breeding seasons combined, 53.8% of families ($N=130$) contained extra-pair sired young and 33.06% of all offspring ($N=484$) were sired by extra-pair males. Ninety-one different males were represented as the social fathers of these 130 families, because for many males we assessed the paternity of their broods in more than one breeding season or in more than one nesting attempt in the same season.

Within-season changes in parentage between successive nesting attempts were estimated from 26 male–female pairs that had two families fingerprinted in the same breeding season and two pairs that had three families fingerprinted. The social father's share of paternity in the brood changed in 18 (60%) of the 30 transitions from one nesting attempt to the next (Table II). Decreases ($N=14$) in parentage (proportion of brood sired) were significantly more likely and were larger than increases ($N=4$; Wilcoxon matched-pairs signed-rank $T^+=20.5$, $z=-2.84$, $P=0.005$). Males' prospects for paternity in re-nests were further diminished because, on average, clutch size declined by 13.6% between nesting attempts (Wilcoxon matched-pairs signed-ranks, $T^+=252.5$, $z=-3.09$, $P=0.002$, clutch size changed for 24 of 34 females), although the decline was attributable to advancing date and not nest succession per se (partial correlation: day of year, $b=-0.02$, $P=0.04$; nest number, $b=-0.14$, $N=118$, $P=0.72$). Importantly, change in clutch size was not related to the incidence of extra-pair paternity in the first nest (Mann–Whitney $U=96$, $z=-0.278$, $N=17,12$, $P=0.78$), the second nest (Mann–Whitney $U=75$, $z=-0.929$, $N=9,21$, $P=0.35$) or to whether the amount of extra-pair paternity increased (Mann–Whitney $U=82$, $z=-0.108$, $N=12,14$, $P=0.91$).

The parentage benefits to breeding adults are also dependent upon the probability of nest success. If nests with extra-pair paternity were more likely to fail, either because of lower paternal care (Weatherhead et al. 1994) or seasonal changes in nest success, then our sample of parental care of cuckolded males could have been biased towards males showing a lesser reduction. This outcome would have made it more difficult to detect a

relationship between paternal care and parentage. Nest success was unrelated to either nesting date or parentage, however. The daily probability of nest survival was 0.957 for clutches of eggs ($N=210$ nests followed), 0.947 for broods of nestlings ($N=57$ nests; calculated according to Mayfield 1961, 1975), and overall, the probability of nest success from clutch initiation through to fledging was 31% ($N=229$ nests followed). Nests initiated before the median clutch initiation date for that year enjoyed similar daily survival probabilities through the egg stage (daily survival probabilities: pre-median=0.973, post-median=0.959, $G=2.40$, $df=1$, $P=0.12$) and nestling stage (pre-median=0.92, post-median=0.969, $G=4.2$, $df=1$, $P=0.04$) as nests initiated after that date, and over the complete nest period the probability of survival did not differ between the two groups ($G=0.14$, $df=1$, $P=0.71$). There was also no difference in the percentage of nests that fledged young between those with extra-pair paternity (75%, $N=20$) and those without (82.4%, $N=17$; $G=0.30$, $df=1$, $P=0.59$). Collectively, the declines in parentage and clutch size, along with the lack of consistent differences in nest success with date and parentage, suggest that males are unlikely to increase their parentage through re-nesting.

Between-season changes in parentage could also influence the relationship between paternity and paternal care. For example, if parentage increased with breeding experience or age, and males increased the likelihood of survival to the next breeding season by reducing their parental care, then males would increase their lifetime reproductive success by adjusting care to paternity. Provisioning nestlings seemed to be costly for males. Twenty-eight of the males whose parental care was observed in 1992 resided in areas that were fully searched the following breeding season: nine (32%) had returned to the same territory to breed and 19 (68%) were not seen. Males that had provided relatively more care to nestlings the previous year were less likely to have returned, independent of when they bred the previous season and whether the nest fledged young (Table III; Fig. 3). We conclude that this difference in return was due to differences in survival and not dispersal, because over the four years of our study, breeding males showed extreme breeding-site fidelity between seasons: all returning males ($N=41$) resided either in the same location as the previous

Table III. Relationship between male return in year $X+1$ and breeding date, fledging success and relative feeding rate in year X

Independent variable	Parameter estimate	χ^2	df	P
Breeding date	-0.068	0.92	1	0.34
Fledged young	-0.718	1.87	1	0.17
Relative provisioning rate	2.074	4.27	1	0.04

The overall logistic regression model is significant ($G=4.214$, $df=3$, $P=0.04$).

year or within a distance equivalent to twice the average territory diameter.

We found no evidence that increasing breeding experience or age was associated with increased parentage. We fingerprinted the broods of eight

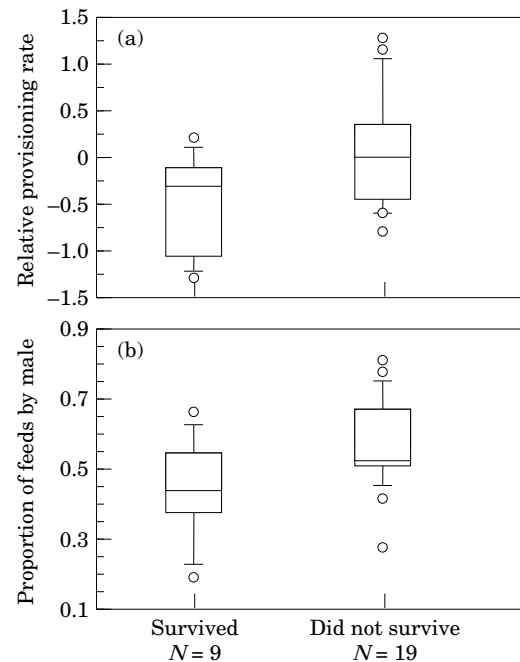


Figure 3. Relative provisioning to nestlings by males that did not survive and those that did survive to the following breeding season. (a) Differences in mean relative male feeding rate controlling for age and number of nestlings (Mann-Whitney $U=45$, $z=-1.20$, $P=0.046$). (b) Differences in proportion of feeds by male (Mann-Whitney $U=40.5$, $z=-2.21$, $P=0.027$). Horizontal lines show medians; vertical lines show standard errors; circles show outliers. See Table III for multivariate analysis.

Table IV. Paternity in successive breeding seasons for the same male. All males mated with a different female in the second year

Second year	First year			
	No extra-pair paternity	Extra-pair paternity		
No extra-pair paternity	0	Higher 4	Lower 0	Same 0
Extra-pair paternity	3	1	0	0

Proportion of young due to extra-pair paternity in the second year is expressed as higher, lower or the same level as in the previous year for males that lost paternity in both years.

males in two successive years. As with repeated breeding attempts in the same season, changes in males' parentage in successive years were common (Table IV). Increases in parentage ($N=4$) with increasing age, however, were neither more likely nor greater than parentage decreases ($N=4$; Wilcoxon signed-ranks $T^+ = 17$, $z = -0.14$, $P = 0.89$). Each of these eight males was initially caught the year we fingerprinted their first family. Because we knew the previous occupants of these territories and because of the strong breeding site fidelity in this population, we conclude that these data derive from the first and second breeding seasons of each of these eight males. Although breeding experience beyond the second year may be important, further evidence against age-dependent increases in paternity in this short-lived passerine comes from males, some in at least their third ($N=6$) or fourth ($N=2$) breeding seasons, whose relative ages could be estimated. For this analysis, we assumed that males were in their first breeding season when first banded and used only data from areas in which we had banded males in the previous two years in order to reduce any bias towards underestimating ages. The incidence of extra-pair paternity did not differ significantly between first year and older males (1 year old = 62.2% cuckolded, $N=45$; >1 year old = 47.6%, $N=21$; $G=1.24$, $P=0.26$), nor did the proportion of extra-pair offspring differ between first-year and older males among nests with extra-pair paternity (1 year old 0.62 ± 0.27 , $N=28$; >1 year old 0.71 ± 0.24 , $N=10$; Kruskal-Wallis $\chi^2=0.95$, $P=0.33$).

A low probability of survival greatly diminishes the chances of increased paternity in future breeding from the perspective of a male who has lost paternity in the current breeding attempt. Overall,

just 29.9% of marked males ($N=137$) returned from one season to the next, and among potential returnees whose paternity was analysed, return was not related to paternity in the preceding season (11 of 30 that lost paternity returned and 9 of 25 with full paternity returned; $G=0.003$, $df=1$, $P=0.96$). Collectively then, evidence from changes in parentage within a breeding season, differences in nest success, changes in clutch sizes, changes in parentage between seasons and probability of survival all suggest that cuckolded males are unlikely to achieve higher parentage in future reproduction.

DISCUSSION

We found no evidence that males provided less parental care when their parentage had been reduced by extra-pair fertilizations. Males with full, partial or no parentage did not differ in how often they fed nestlings or in the proportion of nestling feeds they provided. These results are seemingly at odds with the dictum that males should be selected to avoid providing care to unrelated offspring, particularly if the association between high relative provisioning by males and reduced male survival represents a cost of providing care. These results are consistent, however, with recent models that predict that the co-evolution of parentage and parental care is sensitive to paternity in subsequent matings.

Why is paternal care unrelated to parentage in yellow warblers? Theory suggests that of the three principal factors determining whether males reduce parental care in response to reduced parentage, paternity in subsequent matings is most important, because it determines whether

there is a future benefit to compensate males for the cost of reducing their current paternal care (Westneat & Sherman 1993). The balancing of costs and benefits can involve complicated trade-offs that are difficult to measure (Lessells 1991). These trade-offs in the current context are limited, because males have just three possible ways to gain paternity: (1) parentage in the current brood, or its replacement, (2) parentage in a future breeding season or (3) extra-pair copulations with other paired females. Evidence outlined below suggests that the increase in benefit attainable through these three routes is negligible and therefore unlikely to exceed the costs, which may explain the absence of paternity-dependent parental care in this population of yellow warblers.

Parentage variation between successive nests of the same pair indicates how the benefit of care varies between nests within a season. Males that re-nested and experienced any change in parentage usually suffered a reduction. Re-nesting was also associated with reductions in clutch size. Nest success did not vary consistently with breeding date or parentage. In the absence of other influences on within-pair reproductive success of which we are unaware, these factors collectively result in the benefit from investment in a current brood exceeding the benefit from investment in a later brood the same season. Thus, selection should favour males that provide parental care despite lower paternity over those that respond to reduced paternity by reducing care in a way that might jeopardize the present brood.

If parentage in subsequent breeding seasons was likely to improve, selection could favour reduced paternal care in response to reduced paternity, but we found no effect of male age or breeding experience on parentage. Individual males' parentage typically changed from one breeding season to the next, but increases and decreases occurred with about equal frequency. Although the lower rate of return of males that provided greater provisioning may reflect the cost of that provisioning, it is equally likely that such a relation could also arise if individuals with a lower likelihood of survival for some other reason, also make a larger terminal investment. Thus, it is questionable whether this relation represents a cost of provisioning and experimental data are needed (Lessells 1991; Pärt et al. 1992). Overall, the probability of survival to the next breeding season was low, which can favour paternity-

independent care (Houston 1995). Thus, the lack of an improvement in parentage between seasons and the low prospects of survival both seem to favour investment in the current brood at the expense of future broods.

Extra-pair mating opportunities could influence male parental care if males face a trade-off between provisioning young and pursuing extra-pair matings (Westneat & Sherman 1993). To produce a pattern of paternity-dependent parental care, however, males with partial parentage must reduce their provisioning to pursue extra-pair matings, but males with full parentage need not reduce their care for such opportunities (Wright & Cotton 1994). This would result if the benefits from extra-pair mating outweighed the costs to offspring for only those males with partial parentage. We found that paternity gained from extra-pair mating can be greater than within-pair parentage, however, and it strongly influences variation in mating success in this population (Yezerinac et al. 1995; S. M. Yezerinac, unpublished data). Thus, all males, regardless of their parentage, probably provision at a level that allows them to pursue extra-pair matings. Results of a supplemental food experiment on yellow warblers support this view; increased food availability produced neither an increase nor a decrease in males' provisioning of nestlings, but did influence female behaviour patterns (Lozano & Lemon 1995). Moreover, although successful extra-pair sires are commonly cuckolded (Yezerinac et al. 1995), not all males are equally successful in siring extra-pair young (Yezerinac 1995, unpublished data), and similar patterns have been shown in other species (Westneat 1988; Morton et al. 1990; Kempenaers et al. 1992; Møller 1994; Mulder et al. 1994; Wetton et al. 1995). Thus, a pattern of parentage-dependent paternal care resulting from a trade-off with pursuit of extra-pair matings may not apply generally.

Pursuit of extra-pair matings could create intraspecific variation in paternal care that is independent of parentage in another way. If, as we hypothesize above, levels of male care are set to allow pursuit of extra-pair matings, then variation in paternal care would increase as the variation between males in their potential to benefit from this strategy increased (Burley 1986, 1988; Møller 1994; Wright & Cotton 1994). The circumstances favouring this strategy could either be ecological or reflect intrinsic differences between males. For

example, males whose mates nest early in the breeding season may have more opportunity to pursue extra-pair matings than males whose mates nest more synchronously. Similarly, some males may be better able to exploit opportunities for extra-pair mating by virtue of the 'quality' of their territory, their own intrinsic 'quality' or breeding experience, or their attractiveness to females (Weatherhead & Boag 1995). The lack of correlation between the amount of care and fledging success suggests that the option exists for males to exploit extra-pair mating opportunities with little or no cost to nestlings. Indirect evidence suggests that intrinsic differences between male yellow warblers explain some of the variation in both extra-pair mating success and paternal care (Studd & Robertson 1985, 1988, 1989; Yezerinac 1995). Hence, variation in male parental care could be related to males' pursuit of extra-pair paternity without any dependence on parentage in their 'own families'.

Providing care for broods in which males have no paternity seems at odds with cost-benefit models, because these males appear not to receive any fitness benefits. Males might be expected to abandon such broods to pursue other mating opportunities or to commit infanticide (Crook & Shields 1985; Freed 1987; Møller 1988a; Davies 1992; Houston 1995) and thereby hasten re-nesting, but we observed neither in this population. Even among nests that were not fingerprinted, there were no cases of male abandonment or evidence of infanticide, although because infanticide may be difficult to observe without systematic efforts (Crook & Shields 1985), we cannot dismiss this possibility. Nevertheless, many males with no paternity provided care to these broods.

We suggest two explanations for this pattern. First, males' accuracy in assessing their parentage is probably low. Male birds seem incapable of distinguishing kin from non-kin in the nest (Burke et al. 1989; Davies 1992; Davies et al. 1992; Lifjeld et al. 1992; also witness interspecific brood parasitism), and when male provisioning to a brood does vary with parentage, kin are not fed preferentially (e.g. Davies 1992). Therefore, it is reasonable to assume that males rely on indirect cues to assess their paternity in the brood (Davies 1992; Møller 1988b; Westneat et al. 1990). Because individuals seeking or engaging in extra-pair matings might be selected to be covert, the quality of information provided by these cues is probably

low. Moreover, males' paternity assessment rules can be imperfect (Davies 1992; Davies et al. 1992). Hence, the absence of abandonment or infanticide and males' vulnerability to complete cuckoldry might occur because males cannot judge accurately when their parentage is zero and, as argued above, there is a cost to making the wrong decision, given the low future paternity prospects.

A second potential explanation for the absence of paternity-dependent care in cases of complete cuckoldry is that the ability to assess parentage may not have evolved (or has been lost) among males in this population of yellow warblers because males would rarely benefit from using that information. Selection for paternity-dependent parental care arises when reducing current investment allows for future investment with higher paternity benefits. Our data on patterns of parentage suggest that males in this population are not experiencing this selection pressure. The absence of paternity assessment in a species where extra-pair paternity is common can be tested with experiments in which males are detained before or during their mates' fertile period (e.g. Hatchwell & Davies 1992a, b), or in which the resident male is removed following fertilization and a replacement male allowed to settle (e.g. Meek & Robertson 1991; Whittingham et al. 1993). If testing a variety of cues known to be used by other species reveals that males do not reduce their parental care in situations where they should be able to judge they have no paternity, then our hypothesis, that males cannot assess their paternity because of the weak selection for this capacity, would gain support.

The lack of parentage-dependent paternal care among yellow warblers is consistent with the hypothesis that future benefits are insufficient to compensate males for costs of reducing paternal care. A weakness of our study for inferring whether selection should favour parentage-dependent care, however, is that we cannot measure what paternity in subsequent broods would be if males were actually to reduce care, because males do not show this pattern of care. Thus, a useful extension of this study would be to force males to reduce their provisioning (without preventing them from re-directing the effort) and then measure parentage in their re-nests. Based upon the current study, we predict similar patterns of declining parentage as reported here and no difference in male provisioning between nests. If parentage were to increase, however, then

attention should be given to parentage assessment and kin constraints as the causes of parentage-independent paternal care. These hypotheses await testing in yellow warblers, as does the general applicability of these hypotheses and the cost-benefit approach to other species in which paternity is not related to paternal care.

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