

Certainty of paternity and paternal investment in eastern bluebirds and tree swallows

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Abstract. Extra-pair paternity is common in many socially monogamous passerine birds with biparental care. Thus, males often invest in offspring to which they are not related. Models of optimal parental investment predict that, under certain assumptions, males should lower their investment in response to reduced certainty of paternity. We attempted to reduce certainty of paternity experimentally in two species, the eastern bluebird, *Sialia sialis*, and the tree swallow, *Tachycineta bicolor*, by temporarily removing fertile females on two mornings during egg laying. In both species, experimental males usually attempted to copulate with the female immediately after her reappearance, suggesting that they experienced the absence of their mate as a threat to their paternity. Experimental males copulated at a significantly higher rate than control males. However, contrary to the prediction of the model, experimental males did not invest less than control males in their offspring. There was no difference between experimental and control nests in the proportion of male feeds, male and female feeding rates, nestling growth and nestling condition and size at age 14 days. We argue that females might have restored the males' confidence in paternity after the experiment by soliciting or accepting copulations. Alternatively, males may not reduce their effort, because the fitness costs to their own offspring may outweigh the benefits for the males, at least in populations where females cannot fully compensate for reduced male investment.

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Birds are unique among vertebrates in that the majority of species are socially monogamous with biparental care being the norm (Lack 1968). Although the extent and the form of paternal care differ between species, males often invest considerably in their offspring, which is costly in terms of time and energy expenditure (Clutton-Brock 1991). As Trivers (1972) pointed out, 'Where male parental care is involved, the male runs the risk of raising another male's offspring'. Although, as Trivers (1972) put it, 'Adaptations should evolve to help guarantee that the female's offspring are also his own', it is now clear that in many species, despite paternity guards such as mate guarding and frequent copulation, nests often contain

young fathered by other, non-related males (Birkhead & Møller 1992; Gowaty 1996).

How should males respond in terms of parental investment in relation to their paternity? In general, males should behave in such a way as to maximize the sum of reproductive success from their current and their future broods. Thus, males should weigh the value of their current brood relative to the value of their subsequent broods and assess how current investment will affect future reproduction (Carlisle 1982; Winkler 1987). Based on this view, Westneat & Sherman (1993) developed a general model which encompassed previous theoretical work and they came to the intuitively appealing conclusion that males should respond to reduced paternity by investing less, at least under certain conditions.

Do males respond in the predicted way? Three types of empirical approach have been used to investigate the relationship between paternity and paternal care. Several studies have related the males' paternity in the brood (as determined with

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molecular techniques) to a measure of those males' contribution to parental care (usually feeding of offspring). The majority of these studies did not find the predicted relationship between paternity and paternal care. However, such studies are inappropriate as tests for the models, because of the many confounding factors that could influence the relationship (for discussion and a review of such studies see [Kempnaers & Sheldon 1997](#)). To avoid (at least some of) these confounding effects one can compare paternity and parental care for the same pair in successive broods within a season (e.g. [Dixon et al. 1994](#); [Freeman-Gallant 1996](#)), but this is possible only in multi-brooded species. Another approach is to manipulate experimentally the male's certainty of paternity and investigate how the manipulation affects his parental investment.

Two types of experiment have been performed in an attempt to manipulate certainty of paternity: temporary male removals (e.g. [Møller 1988, 1991](#); [Davies et al. 1992](#)) and temporary female removals (e.g. [Wright & Cotton 1994](#); [Sheldon et al. 1997](#)). The aim of such experiments is not necessarily to change paternity in the brood (although some studies did change paternity and were designed to do so, e.g. [Davies et al. 1992](#)), but to change the male's perception of his female's fidelity. The type of experiment that is performed should depend on the extra-pair behaviour of the species. For example, in species where females actively seek extra-pair copulations, temporary female removals are used to mimic the natural situation more closely. Males, in this situation, may use the absence of their mate as a cue to assess their paternity.

We studied the response of males to the temporary absence of their fertile female in two species, the eastern bluebird, *Sialia sialis*, and the tree swallow, *Tachycineta bicolor*. Both species are well studied: they are socially monogamous, but extra-pair paternity is common ([Gowaty & Bridges 1991](#); [Meek et al. 1994](#); [Barber et al. 1996](#)). For both species, there is evidence that females seek extra-pair copulations by visiting other males ([Gowaty & Bridges 1991](#); B. Kempnaers, personal observation). Male eastern bluebirds guard their fertile mates ([Gowaty et al. 1989](#); [Meek & Robertson 1994a](#)), but a male-removal experiment did not result in lower investment by experimental males (E. A. MacDougall & R. J. Robertson, unpublished

data). Mate guarding in tree swallows is very weak ([Leffelaar & Robertson 1984](#); [Chek & Robertson 1994](#)), but males may use frequent copulations to protect their paternity ([Venier & Robertson 1991](#)). A correlational study on the relationship between paternity and paternal care ([Lifjeld et al. 1993](#)) and a male-removal experiment ([Whittingham et al. 1993](#)) showed no effect of (certainty of) paternity on subsequent male investment.

Our aim in this study is to test the prediction from [Westneat & Sherman's \(1993\)](#) model that males should expend less parental effort when their certainty of paternity within a brood is low. This prediction relies on several assumptions (see [Westneat & Sherman's](#) hierarchical organization in their Table 3). First, we assume that individuals are able to assess their parentage, that is, that they respond to changes in their 'certainty of paternity' for a specific brood. Second, we assume that males are not able to assess relatedness to individual offspring in the nest. Finally, we assume that males use the absence of their mate as a cue to assess their paternity. When the certainty of paternity for the current brood is experimentally lowered, the model predicts that the optimal male parental effort should be reduced, because males should be able to do better in a future brood.

Here, we first describe how male eastern bluebirds and tree swallows responded after the female was released from captivity by comparing copulation behaviour of control and experimental pairs. Second, we describe male and female parental investment (i.e. the proportion of male feeds and feeding rates) in control and experimental broods. Third, we compare brood success and nestling growth and condition in both groups.

METHODS

Study Area and General Methods

We carried out the study in 1995 near the Queen's University Biological Station (44°34'N, 76°19'W), Chaffeys Locks, Ontario, Canada. From March to July, we studied a population of eastern bluebirds breeding in nestboxes. The nestboxes were put up in 1988 along different roads in the vicinity of the Biological Station (the trail included nestbox grids set up for tree swallows: see below). From mid March onwards we checked the area at least twice a week to record the arrival of birds. We captured the majority of males, soon

after their arrival in their territory, using mist nets in combination with song playback and a mounted male, or a nestbox trap, or by trapping the roosting male in the box at night. To avoid causing desertion, we caught females only after the young hatched (in eastern bluebirds, the sexes can be easily distinguished in the field). We checked nestboxes in occupied territories at least twice a week until nest building was almost complete and daily from then on until the female started incubation. Around the hatching date, we visited nestboxes at least once a day until all young had hatched and we made further visits to weigh the young when they were 1, 3, 4, 6, 8, 10, 12 and 14 days old (when all young did not hatch on the same day, these days represent the age of the majority of the young). Three weeks to 1 month after hatching, we checked whether the young had fledged. We trapped feeding parents inside the box when the young were 7 days old. We ringed all adults with a metal band from the Canadian Wildlife Service (CWS) and a unique combination of three colour bands. Some males also received a plastic coloured leg-streamer (about 15 mm long) glued on one of the colour bands to facilitate quick recognition in the field. We aged the adults based on the shape and colour of the 10th primary wing coverts (second-year or after-second-year, see [Pitts 1985](#); [Plissner et al. 1994](#)), one of which was collected for later reference. We banded all 8-day-old nestlings with a metal CWS band.

From April to July, we studied tree swallows breeding on different nestbox grids and in solitary boxes along the road from the grids to the Biological Station. In this study we used three grids: RF ($N=6$ boxes) and TG ($N=8$ boxes) put up in 1985 with boxes 40 m apart along rows and 28 m apart along diagonals between rows and the new grid JG with 31 boxes, put up 30 m apart along rows with 30 m between rows. For our experiments, we used pairs breeding in grids and in solitary boxes and pooled the data, because there was no difference in the frequency of extra-pair paternity between pairs breeding solitarily or in grids ([Dunn et al. 1994](#)). We inspected all grids and solitary boxes almost daily. As soon as adult birds were present inspecting the nestboxes, we started trapping them with mist nets or inside their boxes after nest initiation. We banded each individual with a metal CWS band and, if we could determine the sex unequivocally (see below),

with a red (female) or a blue (male) colour band. We marked each individual with a unique combination of coloured spots on the wings and/or tail using acrylic paint. We determined sex and age (second-year or after-second-year) based on plumage characteristics and wing chord (see [Hussell 1983](#); [Stutchbury & Robertson 1987](#)) and later checked the sex by the presence of a brood patch (females) or cloacal protuberance (males) and via behavioural observations. We checked nestboxes and weighed the chicks following the same schedule as described above for the bluebirds. To help identify parents during feeding observations (see below), we recaptured parents when the young were 3 days old and coloured their white breast feathers with a felt-tip ink marker (green for males and red for females).

After catching an adult bird, we measured each wing to the nearest 0.1 mm using a ruler and each tarsus to the nearest 0.01 mm using digital calipers. We weighed adult birds with a Pesola spring balance to the nearest 0.1 g and chicks with an electronic balance (accurate to 0.1 g). We also measured each wing and tarsus of all 14-day-old chicks.

Experimental Procedure

For both species, we removed females temporarily on two mornings during the egg-laying period by trapping them inside their box. Removals were carried out on days 1 and 2, where day 0 is the day the first egg is laid. Thus, females were removed at a time when copulations are frequently observed in tree swallows ([Venier & Robertson 1991](#)) and in eastern bluebirds (personal observations). The experiment was also designed in such a way that males were unable to copulate with their female during the 'insemination window', that is, the short (60-min) period just after egg laying when the next egg is fertilized ([Cheng et al. 1983](#)). Although [Birkhead et al. \(1996\)](#) showed that the insemination window does not represent a general peak in female fertility, a copulation during this time can result in the fertilization of the next ovum to be ovulated.

We caught females after they entered the box in the morning (eastern bluebirds and tree swallows) or at night when they were roosting inside the box (tree swallows). We plugged the entrance hole of the box with a sock and covered the box with a dark cloth. We removed boxes attached to metal

Table I. Breeding parameters of experimental and control nests of eastern bluebirds and tree swallows

	Control	Experiment	Statistical test†‡
Eastern bluebirds			
Number of nests	10	7	
Laying date*	113.3 ± 3.5	111.1 ± 2.7	$t=0.45, NS$
Clutch size	5.2 ± 0.3	4.7 ± 0.3	$t=1.15, NS$
Proportion eggs hatched	0.89 ± 0.08	0.81 ± 0.07	$U=48.5, NS$
Number of fledglings†	3.7 ± 0.6	2.6 ± 0.6	$t=1.23, NS$
Tree swallows			
Number of nests	21	25	
Laying date*	138.6 ± 1.3	137.4 ± 0.9	$t=0.79, NS$
Clutch size	5.48 ± 0.16	5.48 ± 0.23	$t=-0.01, NS$
Proportion eggs hatched	0.86 ± 0.05	0.86 ± 0.04	$U=282, NS$
Number of fledglings†	3.7 ± 0.5	3.8 ± 0.4	$t=-0.21, NS$

Data are $\bar{X} \pm SE$.

*1 January=1, 1 April=91, 1 May=121.

†Unsuccessful nests, (i.e. nests that produced no fledglings) are included.

‡Student's t -test or Mann-Whitney U -test.

poles (almost all tree swallow and some bluebird boxes) and replaced them with similar boxes containing nests and eggs collected from abandoned nests. For boxes that could not be removed (most bluebird boxes) we attached the replacement box to the original, completely covered box. In a few cases we used dummy eggs made from plasticine to resemble real eggs. Bluebird and tree swallow eggs do not show obvious inter-individual differences and it is therefore unlikely that males could recognize the eggs as not belonging to their mate.

Female bluebirds were kept inside their box until about 0940 hours (Eastern Standard Time) for an average duration of 161 min (range 100–206); female tree swallows were kept in the box until about 0800 hours EST. In this way, most (if not all) females were kept in captivity until at least 1 h after they had laid their egg (most bluebirds laid their eggs between 0700 and 0900 hours EST, Meek & Robertson 1995; tree swallows never laid later than 0705 hours EST, Venier & Robertson 1991). We replaced the original nestbox and released the female from a distance of about 20 m using a fishing line to pull out the sock.

Nests of both species were alternately assigned to a control and an experimental group to control for a possible date effect. If more than one nest had its first egg on a given day, the decision to assign it to the control or experimental group was also determined by the position of the nestbox, so

that experimental and control nests were more or less equally divided over the different areas (roads, grids and solitary nests). We did not manipulate control birds.

For this study, we used 20 pairs (12 control, 8 treatment) of eastern bluebirds and 50 pairs (22 control, 28 treatment) of tree swallows. Four eastern bluebird pairs (two control, two treatment) deserted after the first day of the experiment (treatment pairs) and after laying one and two eggs (control pairs). One treatment pair re-nested in a nearby box and was subsequently used in the study. Four tree swallow pairs deserted their nests during egg laying: one experimental and one control nest were taken over by wrens, *Troglodytes aedon*, the female of one experimental pair was killed by a hawk (A. Blicek, personal observation) and another female of an experimental nest disappeared.

Experimental and control nests used in our analyses did not differ in clutch size, laying date, hatching success and fledging success (Table I). Laying interruptions occurred in three control eastern bluebird nests and in 10 tree swallow nests (six experimental, four control). For both species, males and females of control and experimental pairs did not differ in age, tarsus or wing length (data not shown). Eight of 10 eastern bluebird control pairs started a second brood, versus two out of seven experimental pairs (Fisher's exact

test: $P=0.058$), which might have been a result of the experiment.

Behavioural Observations

We observed 15 eastern bluebird pairs (eight experimental and seven control) and 48 tree swallow pairs (28 experimental and 20 control) on the mornings of days 1–4 (where day 0 is the day the first egg was laid). We observed eastern bluebird pairs on average for 12 h 16 min (range 5 h 15 min–19 h 22 min), tree swallow pairs on average for 5 h 47 min (range 1 h 49 min–11 h 46 min). We attempted to follow all pairs until 1 h after the female had been released (experiment) or 1 h after the female emerged from the box after having laid her egg (control). To determine when the female had laid the egg in the control boxes, we checked the box after each female visit. We continuously recorded the behaviour of one or both pair members using a hand-held tape-recorder and a watch to note the time. We attempted to follow both the male and the female and recorded behaviour such as feeding, flights, copulations and interactions with other birds. We also recorded the position (distance) of the birds relative to each other and to the nestbox, including the time when one or both pair members were out of sight. Observations of a single pair were often carried out by two observers, so that each could follow one pair member. We considered a copulation successful when we observed cloacal contact. In tree swallows, one copulation usually consisted of a bout of cloacal contacts in quick succession. If females refused to copulate, males often attempted to copulate several times in quick succession. For analyses, we considered such repeated attempts at copulating as one attempt. We also included only those observations where we were able to follow at least one of the pair members for a minimum of 50 min after the female emerged.

Measuring Parental Investment

In the tree swallow and the eastern bluebird, only females build the nest and incubate. Male tree swallows collect and deliver feathers to the nest during the egg-laying and incubation stage and male eastern bluebirds 'courtship feed' the female during egg laying and incubation. However, the males' main parental investment is feeding the offspring, a task shared with the female.

As a measure of parental investment, we counted the number of feeding trips made by the male and the female during 1-h (tree swallows) or 2-h (eastern bluebirds) sessions. Observations were made throughout the day, but not during periods of heavy rain or when the birds were obviously disturbed (e.g. by agricultural work or by birds of prey). Observation sessions for control and experimental broods were spread evenly over the day to control for a possible effect of time of day on parental feeding. For all control and experimental nests, we made observations when the young were 4, 6, 8, 10, 12 and 14 days old. Visits where the male did not enter the box, but either gave the food to the young in the box or to the female, were considered as feeding trips. Only eastern bluebird males gave food to the female: in six cases the female was in the box, in two cases she was near the box but brought the food to the young afterwards. Visits where male or female bluebirds entered the box without a prey item (checked with binoculars or with a spotting scope) were not considered feeding trips. We made all observations from inside a car or sitting in the field 20–50 m from the box. There is no reason to assume that our presence influenced the behaviour of the birds. In some nests, all young died before age 14 days, so observations were not available for all age categories (e.g. in one experimental nest of eastern bluebirds the 13-day-old nestlings died when house sparrows, *Passer domesticus*, took over the nestbox). We excluded data from two control nests of eastern bluebirds where the male disappeared (died?) before the young hatched. No experimental pairs deserted a completed clutch or brood.

Males may change their investment, not by reducing their feeding frequency, but by bringing less food per feeding trip or by bringing food of lower quality. We did not check this directly by measuring the amount or quality of food provided by each sex, but we did investigate the effect of male and female investment on the growth of the offspring.

Data Analyses

To compare paternal investment between experimental and control males, we first considered the proportion of male feeding trips (relative to the total number of feeding trips) calculated as the average proportion over the six observation sessions. The proportion of male feeding trips is

obviously dependent on the investment by the female and the latter might have been influenced by the experiment. Thus, we also compared the feeding rates of males and females separately when nestlings were 4, 6, 8, 10, 12 and 14 days old. In these analyses, we controlled for the number of chicks in the nest by calculating the number of feeds per h and per chick.

To compare the size (wing and tarsus length) of nestlings, we first averaged the measurements from the left and the right side and then calculated average values for each nest. We did not use our measurements to assess the pattern of fluctuating asymmetry. Teather (1996) showed that tarsus and wing length measurements from tree swallow nestlings were not suitable for assessing fluctuating asymmetry and that fluctuating asymmetry was not related to parameters of growth. As a measure of the condition of 14-day-old nestlings, we used the residuals of the linear regression of body mass on size (tarsus length).

Data were analysed using the software packages SPSS/PC+, SigmaStat and StatXact, following Sokal & Rohlf (1995). Proportions and count data (number of feeds) were analysed after angular and square root transformation, respectively. After transformation the data satisfied the assumptions of the parametric tests used. All tests are two-tailed. Data shown in the text are mean \pm SE.

Ethical Note

We kept female eastern bluebirds and tree swallows in the nestbox for a longer than usual time during the egg-laying period. However, we designed the experiment as described above to minimize stress or disturbance for the birds during this critical period. We did not handle the birds and we kept the box in darkness during the entire experiment. Experimental females never tried to escape from the box (which we would have noticed during the handling of the box) and they did not desert their nest more often than control pairs.

RESULTS

Male Behaviour During Egg Laying

In both species, males were clearly aware of the absence of their mate. In eastern bluebirds,

control males closely followed their mate and when she went inside the box, the male stayed nearby and often provided courtship feeding. After the female removal, males approached the box and sometimes inspected it. After a while, all experimental males started calling and singing and they patrolled their entire territory often sitting high up in trees or on poles. Control males rarely called or sung and never patrolled their territory. In tree swallows, experimental males spent more time near the box than control males and they frequently inspected the box or sat inside the box. Some experimental males attracted a new female during the absence of the original female. Invariably, these females left or were chased away by the original females after their release.

Copulation and Courtship Behaviour

If males perceived the absence of their fertile female as a threat to their paternity, then we expected them to try to copulate with the female after she emerged again to minimize the risk of losing paternity (retaliatory copulations; Birkhead & Møller 1992). Therefore, we compared the copulation behaviour of experimental and control males after female emergence. We also expected that experimental male eastern bluebirds would provide less courtship feeding to their mate after she emerged in comparison to control males.

In eastern bluebirds, we observed at least one male copulation attempt immediately after the female was released in every experiment where we could follow the pair ($N=12$). In 10 out of those 12 cases, the first copulation attempt was observed within 60 s of the female being released. The majority of these attempts (79% of a total of 15) were successful. In contrast, copulation attempts were seen in only three out of 11 control observations and none occurred within 20 min of the female leaving the nestbox; two out of four attempts were successful. The copulation rate (number of copulations/attempts per h) was significantly higher for experimental males than for control males (Table II). During the same observation periods, experimental males provided courtship feeding less often than control males, but the difference was not significant (Table II).

In tree swallows, males attempted to copulate after the female was released in 87% of 52 experiments for which we have observational data. Of

Table II. Copulation and courtship behaviour for experimental and control pairs after the female emerged from the nestbox

Observations	Control	Experiment	U^*	P^\dagger
Eastern bluebirds	$N=6$	$N=8$		
Copulation attempts/h	0.42 ± 0.20	1.19 ± 0.19	41	0.01
Copulations/h	0.33 ± 0.17	0.94 ± 0.06	43	<0.01
Courtship feeding/h	1.14 ± 0.48	0.70 ± 0.31	30	NS
Tree swallows	$N=22$	$N=27$		
Copulation attempts/h	1.27 ± 0.39	2.39 ± 0.31	432.5	<0.01
Copulations/h	0.80 ± 0.24	1.56 ± 0.22	428	<0.01
Mean number of cloacal contacts per copulation	5.13 ± 0.47 ($N=11$)	6.46 ± 0.81 ($N=23$)	155.5	NS

Data from days 1 and 2 (days on which experiments were performed) are combined.

Data shown are mean \pm SE.

*Mann-Whitney U -test.

†Corrected for ties.

all 127 copulation attempts by experimental males, 65% were successful. In contrast, control males attempted to copulate in only 37% of 35 observations and 61% of 38 were successful. While the copulation rate was again significantly higher for experimental males than for control males (Table II), the average number of cloacal contacts per successful copulation did not differ significantly between groups (Table II).

Parental Investment

For both species, the male's share of feeding did not differ between the experimental and control pairs (Fig. 1). Although our sample sizes are relatively small, a power analysis showed that a difference between control and experimental pairs of at least 0.19 for eastern bluebirds and 0.08 for tree swallows would have been detected (i.e. statistically significant) with a probability $P > 0.8$ for $\alpha = 0.05$. Given that the experimental males of both species on average fed slightly more than the control males and not less as predicted (Fig. 1), there is no problem with our interpretation that the experiment did not influence paternal investment.

In eastern bluebirds, the male and female feeding rates did not differ between control and experimental pairs (Fig. 2; males: $F_{1,13} = 0.164$, NS; females: $F_{1,13} = 0.517$, NS). Male feeding rates did not increase with chick age ($F_{5,64} = 1.80$, NS), while female feeding rates did ($F_{5,64} = 3.87$, $P < 0.01$). For both sexes, there was no significant interaction

between experiment and age (males: $F_{5,64} = 1.68$, NS; females: $F_{5,64} = 1.44$, NS).

Similarly, in tree swallows, male and female feeding rates did not differ between control and experimental pairs (Fig. 3; males: $F_{1,42} = 1.10$, NS; females: $F_{1,42} = 0.039$, NS). For both sexes, feeding rates increased significantly with chick age (males: $F_{5,203} = 12.65$, $P < 0.0001$; females: $F_{5,203} = 21.03$, $P < 0.0001$), but there was no interaction between age and experiment (males: $F_{5,203} = 0.82$, NS; females: $F_{5,203} = 0.40$, NS).

Nesting Success and Offspring Growth

Brood success, measured as the proportion of hatched eggs that resulted in fledglings, was not affected by the experiment (bluebirds: control, 0.91 ± 0.09 ; experiment, 0.82 ± 0.11 ; $t_{11} = 0.935$, NS; swallows: control, 0.92 ± 0.04 ; experiment, 0.87 ± 0.05 ; $t_{38} = 0.958$, NS). The growth curves of nestlings from control and experimental nests did not differ in eastern bluebirds (Fig. 4), nor in tree swallows (Fig. 5). In tree swallow broods where females reared their offspring alone, chicks grew considerably slower (Fig. 5).

Mean nestling condition at age 14 days did not differ between control and experimental pairs in eastern bluebirds ($t_{11} = -1.18$, NS; Fig. 6a), nor in tree swallows ($t_{38} = 0.19$, NS; Fig. 6b). Similarly, the average wing length of 14-day-old nestlings did not differ between control and experimental pairs (bluebirds: $t_{11} = 1.38$, NS; Fig. 7a; swallows: $t_{38} = -1.42$, NS; Fig. 7b).

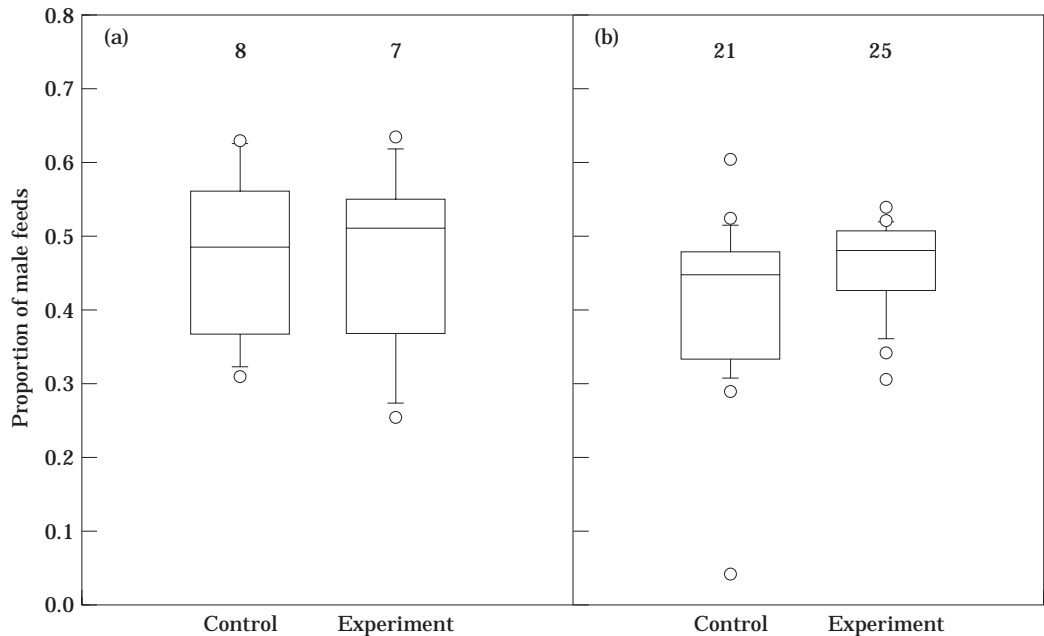


Figure 1. The proportion of feeding trips averaged over all nestling ages by (a) male eastern bluebirds and (b) male tree swallows in experimental and control pairs. Box plots show median (line in the middle), 25% and 75% percentiles (lower and upper end of the box), 10% and 90% percentiles (whiskers) and all data points falling outside the 5% and 95% percentiles; numbers at the top indicate sample sizes. The male's share of feeding did not differ between groups (bluebirds: $t_{13}=0.090$, NS; tree swallows: $t_{44}=-1.65$, NS).

DISCUSSION

In this study, we experimentally investigated the relationship between the male's perceived certainty of paternity and his subsequent investment in the brood, using two small passerines in which extra-pair paternity occurs frequently. Earlier paternity studies (using DNA fingerprinting) of these same populations indicated that 24% of 21 eastern bluebird nests contained extra-pair young (Meek et al. 1994) and between 50 and 92% of tree swallow nests contained extra-pair young (Barber et al. 1996 and references therein). Thus, in these species, males should be under selection to avoid investing in non-related offspring. We attempted to reduce a male's perceived certainty of paternity by temporarily removing his fertile female. Under a number of reasonable assumptions, a theoretical model predicts that males should respond by investing less in their offspring (Westneat & Sherman 1993). However, for both species studied, we did not find any effect of our experiment on paternal investment. In a similar

experiment on the collared flycatcher, *Ficedula albicollis*, Sheldon et al. (1997) did find that males lowered their investment, but the effect was rather weak. We now discuss the possible reasons for the absence of the predicted male response in eastern bluebirds and tree swallows.

Was the Males' Perceived Certainty of Paternity Reduced?

Perhaps males did not change their investment because their certainty of paternity was not affected by the experiment. It is unlikely that our experiment changed the actual paternity in the brood, and, if it did, the prediction would be that the experimental males would have lost less paternity than the control males, because females could not copulate with an extra-pair male during the experiment. This is in contrast to male-removal experiments, where paternity may be directly affected (e.g. MacDougall-Shackleton et al. 1996). However, the actual change in paternity is not important, unless males can directly assess their

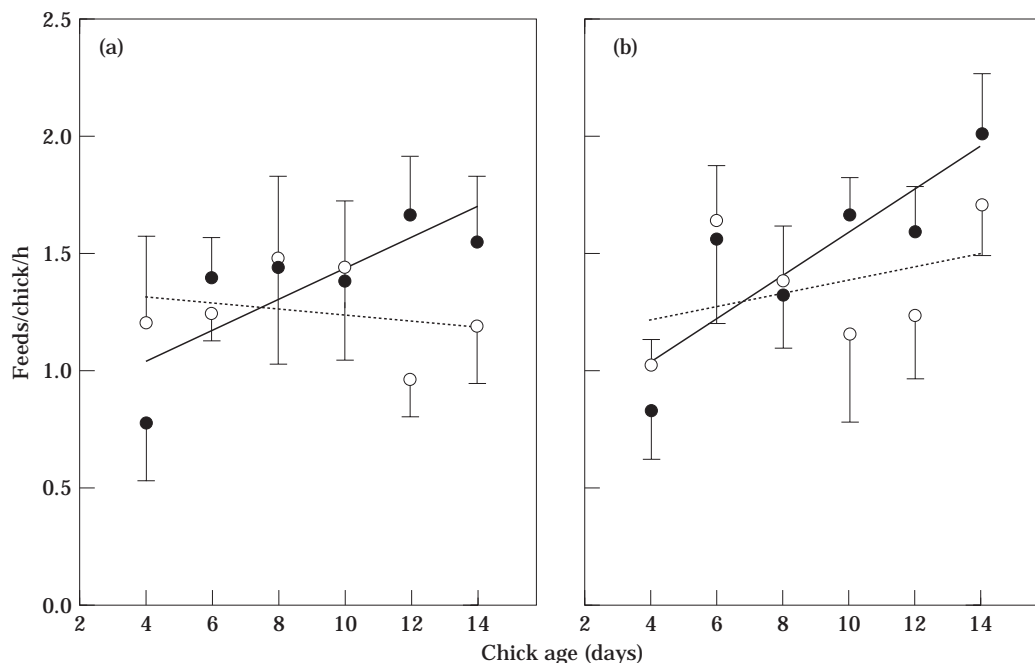


Figure 2. Feeding rates ($\bar{X} \pm \text{SE}$) in relation to chick age for (a) male and (b) female eastern bluebirds. ○: Control pairs ($N=8$); ●: experimental pairs ($N=7$, except for chick age 14 where $N=6$). The lines (· · ·: control; —: experimental) represent the linear regression lines and are drawn only to ease interpretation of the figure.

paternity from offspring characteristics (which is highly unlikely, see [Kempnaers & Sheldon 1996](#)). Rather, it is important how males perceive their paternity and experiments should therefore be designed in such a way that they are likely to change the males' perceived certainty of, or confidence in, paternity. Unfortunately, we do not know which cue(s) males use to assess their paternity, except for a few species. When an experiment is successful in affecting the male's share of parental care, we can safely assume that we changed the male's perceived certainty of paternity and we may get an idea about the cue(s) males use. If the experimental manipulation did not affect male investment, however, we do not know whether this is because we were unsuccessful in changing his perceived certainty of paternity or because of some other reason (as discussed below). This is a problem inherent to experiments designed to lower the male's perceived certainty of paternity. Males may use cues that have not been influenced, or the experimental manipulation might have been too weak to mask the natural variation in perceived certainty of paternity. For example, exper-

iments performed during the laying period may have little effect if males assess their paternity before egg laying (see also discussion in [Sheldon et al. 1997](#)), which is likely if extra-pair copulations performed before the start of egg laying are more effective in fertilizing eggs (see [Colegrave et al. 1995](#)).

What cues might males use to assess their paternity? Observations and temporary male-removal experiments showed that in poly(gyn)androus dunnocks, *Prunella modularis*, and alpine accentors, *Prunella collaris*, the male's investment in the offspring is directly related to the proportion of time he had exclusive access to the fertile female ([Davies et al. 1992](#); [Hartley et al. 1995](#)). Thus, it seems that in those species males use their share of matings with the female as a cue to assess their paternity. If socially monogamous species use a similar cue (time spent with their female), then both a male- and a female-removal experiment should lower their confidence of paternity. Male-removal experiments in both eastern bluebirds and tree swallows did not, however, show any effect on male parental investment

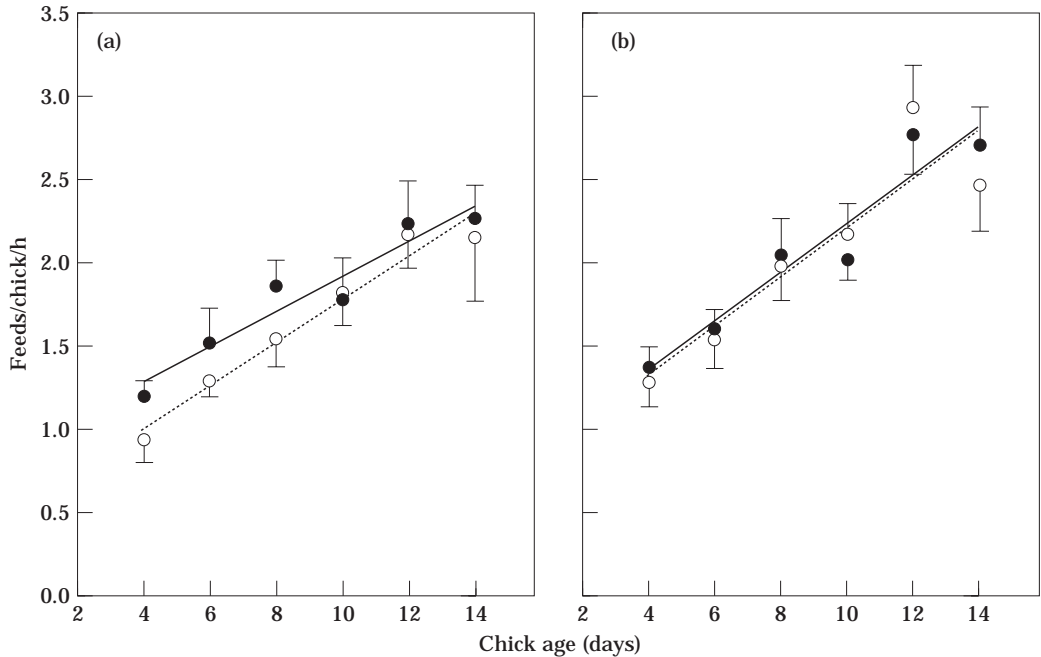


Figure 3. Feeding rates ($\bar{X} \pm \text{SE}$) in relation to chick age for (a) male and (b) female tree swallows. \circ : Control pairs (sample size changes from 19 for chick age 4–10 to 17 for chick age 12–14); \bullet : experimental pairs (sample size changes from 25 for chick age 4–10, 24 for age 12 and 23 for age 14). The sample size of the control group differs from that in Fig. 1b, because two nests were excluded in this analysis: one where the male was seen feeding during only one of six observation periods (see outlier on Fig. 1b) and one nest with only one young that died 8 days after hatching. The lines (\cdots : control; $—$: experimental) represent the linear regression lines and are drawn only to ease interpretation of the figure.

(Whittingham et al. 1993; E. A. MacDougall & R. J. Robertson, unpublished data). In the latter study, males were placed in cages with one-way glass facing their nestbox, so that they could see their mates engage in extra-pair copulations. Whittingham et al. argued that their experiment increased the rate of extra-pair copulations by fertile females, and, as a consequence, it also decreased the confidence of paternity of captive males. However, this is assuming that those males paid attention to their mates, which is not necessarily the case. On the other hand, Møller (1988) concluded that in colonially nesting barn swallows, *Hirundo rustica*, males apparently estimate their paternity from the interest that neighbouring males were taking in their mates during the fertile period. Similarly, Wright & Cotton's (1994) experimental results suggest that male European starlings, *Sturnus vulgaris*, pay attention to the behaviour of their mate. They showed that males reduced their investment when their fertile female

was temporarily placed in a cage next to a decoy male within their sight. Our study suggests that the absence of the female on the mornings when the third and fourth egg were fertilized did not change the males' perceived certainty of paternity in eastern bluebirds and tree swallows.

We attempted to reduce the male's perceived certainty of paternity by temporarily removing his fertile mate during the early egg-laying stage. In tree swallows, extra-pair copulations are observed during that period (Venier et al. 1993) and copulations at that time can lead to fertilizations (Lifjeld & Robertson 1992). In both species, the responses of our experimental males clearly suggested that they experienced the absence of their mate as a threat to their paternity. As expected if they behave to counteract this threat, male bluebirds and swallows tried to copulate with their mate, usually immediately after she reappeared. This differed considerably from the response of the control males, which seldom attempted to

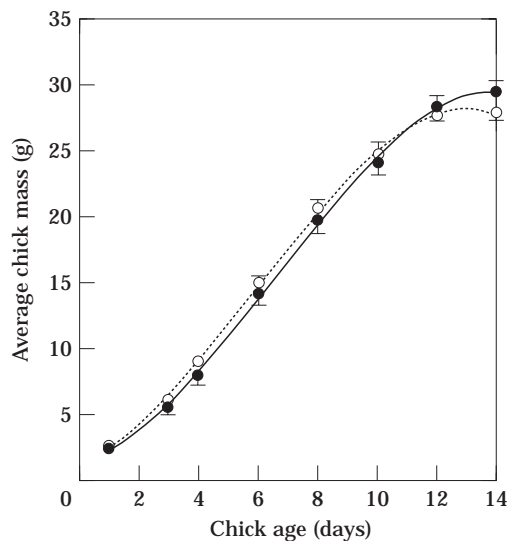


Figure 4. Growth curves (mean chick mass + SE) for eastern bluebirds from control (○) and experimental (●) broods. Sample sizes are the same as in Fig. 2. Third order regression lines were fitted through the data: for control broods (· · ·): average chick mass = $1.072 + 0.938(\text{age}) + 0.335(\text{age})^2 - 0.019(\text{age})^3$, $R^2 = 0.999$; experimental broods (—): average chick mass = $1.770 + 0.208(\text{age}) + 0.429(\text{age})^2 - 0.022(\text{age})^3$, $R^2 = 1.00$.

copulate following the reappearance of their mate after she had spent a considerable amount of time inside the nestbox. Moreover, during the time the female was kept in the nestbox, we observed that eastern bluebird males strongly increased their singing rate, spent more time higher in the trees and made more long flights (unpublished data). Copulation rates in experimental tree swallow pairs were also much higher than those reported in a behavioural study at a similar stage during breeding (see Figure 1 in Venier & Robertson 1991). Male within-pair copulation attempts after separation from their fertile female have been reported in other species and can be considered as a mechanism to protect paternity (e.g. Møller 1987; Aguilera & Alvarez 1989; see also Birkhead & Møller 1992).

In eastern bluebirds, almost all experimental males for which we have good behavioural data successfully copulated with the female and it often appeared as if the female was soliciting the copulation (B. Kempnaers & R. B. Lanctot, personal observation). In contrast, we never observed female tree swallows solicit a copulation

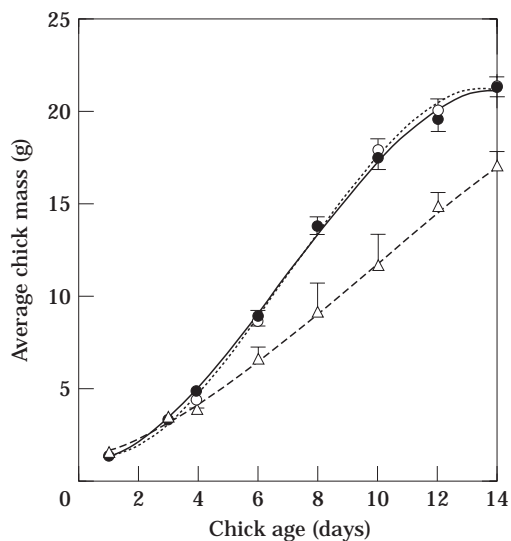


Figure 5. Growth curves (mean chick mass + SE) for tree swallows from control broods (○, $N=19$ for chick age 1–10, $N=17$ for age 12 and 14), experimental broods (●, $N=25$ for chick age 1–10, $N=24$ for age 12 and $N=23$ for age 14) and broods where the female reared the chicks alone (△, $N=3$ for age 1–10, $N=2$ for age 12 and 14). Third order regression lines were fitted through the data: for control broods (· · ·): average chick mass = $1.428 - 0.459(\text{age}) + 0.394(\text{age})^2 - 0.019(\text{age})^3$, $R^2 = 0.999$; experimental broods (—): average chick mass = $0.974 + 5.442(\text{age}) + 0.313(\text{age})^2 - 0.015(\text{age})^3$, $R^2 = 0.998$; no-male broods (---): average chick mass = $1.030 + 0.438(\text{age}) + 0.096(\text{age})^2 - 3.276(\text{age})^3$, $R^2 = 0.998$.

and female tree swallows more often refused to copulate, even after the experiment. Females might want to copulate after the experiment for several reasons: (1) they might need the sperm to avoid infertile eggs; (2) they might want the male to be the father of their offspring; (3) they might want to assure the male that he is the father of the offspring to avoid losing his help; or (4) they might want to avoid male aggression (see below). However, only the last two hypotheses satisfactorily explain why females should solicit immediately after release, because the egg for the next day must have been fertilized already. We observed one case where a female eastern bluebird copulated with the male immediately after being released, but then refused to copulate again. The male attempted to copulate three more times and then became

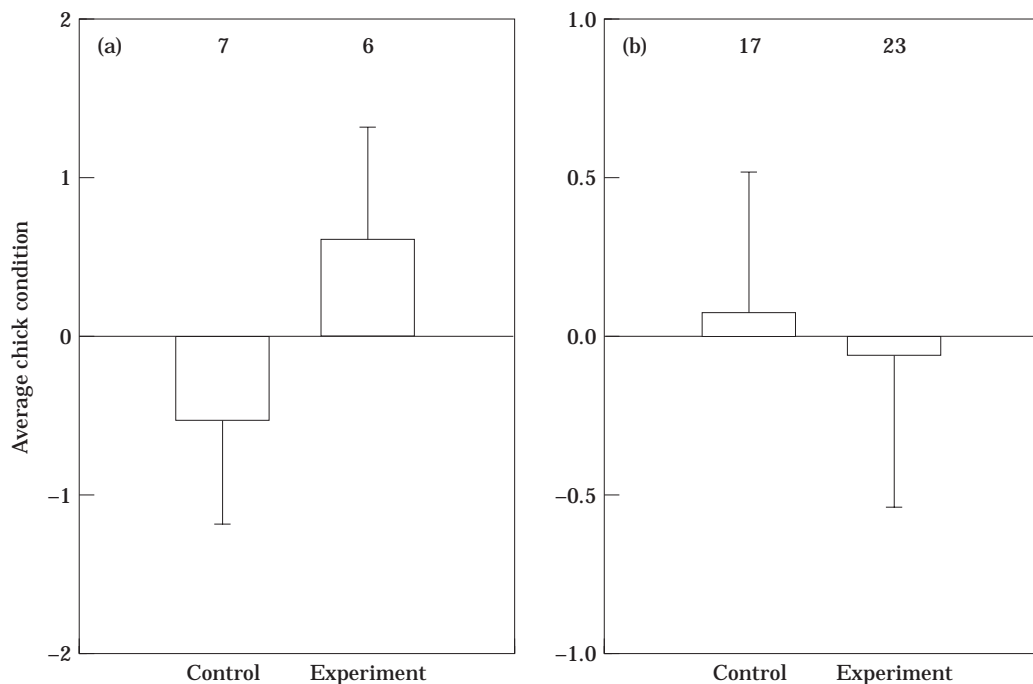


Figure 6. Average chick condition at age 14 days (residuals of the regression of body mass over tarsus length) for control and experimental nests in (a) eastern bluebirds and (b) tree swallows. Numbers at the top indicate sample sizes.

very aggressive, chasing the female around the territory. Coincidentally, this male provided the lowest share of feeds of all males (only 26% of all feeding trips). It is generally accepted that females use solicitation of copulations to assure males that they are the father of the offspring (e.g. [Gjershaug et al. 1989](#)). After female eastern bluebirds lost their mate they frequently solicited copulations from a replacement male, apparently in an attempt to persuade him to stay and feed the offspring (e.g. [MacDougall-Shackleton et al. 1996](#)). In conclusion, our experiment might have reduced the confidence of paternity, but by soliciting copulations female eastern bluebirds might have restored the male's confidence. This argument does not apply for the tree swallows, because experimental females were not more likely to solicit copulations than control females. On the other hand, experimental males attempted to copulate more frequently after the females emerged and thus in total obtained more copulations than control males.

Did we Fail to Detect a Reduction in Male Investment?

Perhaps males did reduce their investment, but we were not able to detect it. We consider this unlikely for several reasons. First, we observed male and female feeding rates over the entire nestling stage (from day 4 to day 14) for a total of 6 h (tree swallows) or 12 h (eastern bluebirds). Thus, we would have been able to detect relatively small reductions in male investment. Second, if males invested less by providing food of lower quality or less food per trip, this should have been reflected in the growth curves of the offspring, unless females fully compensated for the decrease in male care. If males reduced their effort by such a small amount that we could not detect it, the reduction is also unlikely to have had an effect on the male's fitness (e.g. his survival probability).

Males might have invested equally in feeding their offspring, but they might have reduced their investment in defence of offspring against predators. We did not measure the latter, but

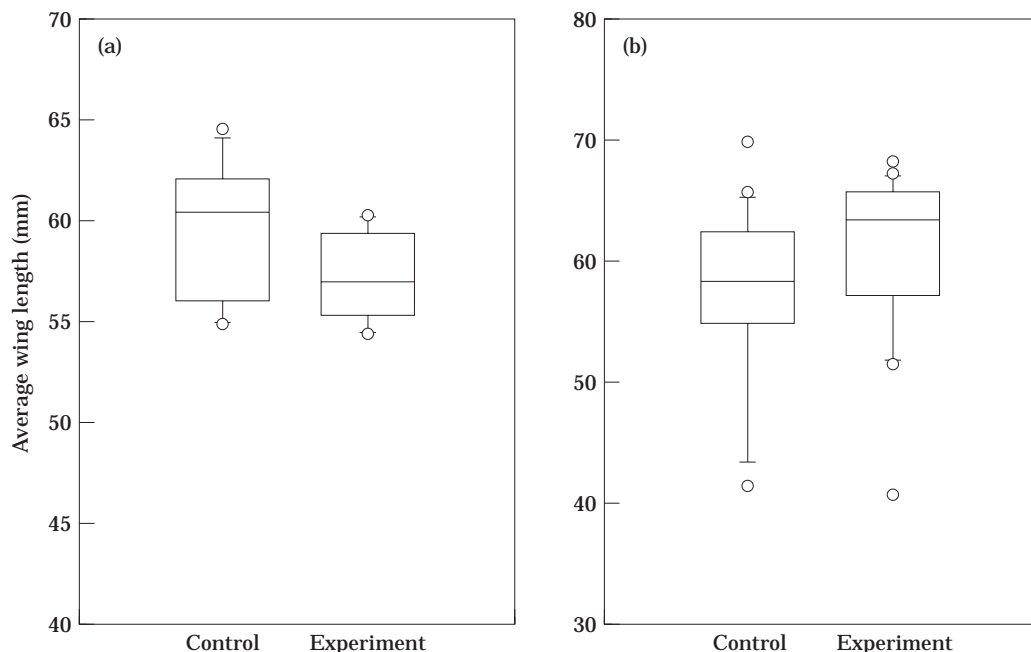


Figure 7. Average wing length (mm) of 14-day-old chicks from control and experimental nests in (a) eastern bluebirds and (b) tree swallows. Box plots show median (line in the middle), 25% and 75% percentiles (lower and upper end of the box), 10% and 90% percentiles (whiskers) and all data points falling outside the 5% and 95% percentiles; sample sizes are the same as in Fig. 6.

Whittingham et al. (1993) did not find any reduction in offspring defence after experimentally removing male tree swallows.

Are our Assumptions Wrong?

We assumed that males are able to assess their paternity for a certain brood, but we do not know whether this is true. If it is not true, there might still be a relationship between the level of paternal care and paternity, but instead of being a direct causal response the relationship would have arisen through evolutionary time (Westneat & Sherman 1993). In such a case, experimental manipulations would not have any effect. A comparative analysis across species of the levels of male investment in relation to the frequency of extra-pair paternity does suggest that such an evolutionary response exists (Møller & Birkhead 1993; see also comment by Dale 1995 and reply by Møller & Birkhead 1995).

We also assumed that males were unable to assess their relatedness to individual offspring. If this assumption is incorrect, males can directly assess their paternity rather than rely on indirect

cues such as the absence of their mate. However, Kempnaers & Sheldon (1996) argued that it is highly unlikely that males can recognize their own offspring in a brood. Leonard et al. (1995) showed experimentally that male and female western bluebirds, *Sialia mexicana*, do not discriminate between their own and unrelated nestlings.

Westneat & Sherman's (1993) model predicts no male response if there is no variation in paternity (i.e. paternity of offspring in the current brood equals paternity of offspring from additional matings equals paternity of offspring in future breeding attempts), even when males are able to assess their paternity. However, it is highly unlikely that for an individual male paternity is invariant. Moreover, assuming that the experiment was successful in lowering the male's perceived certainty of paternity, we introduced variation and thus the model predicts an effect.

Costs and Benefits of Parental Care

Whittingham et al. (1992) and Westneat & Sherman (1993) concluded independently that the

effect of paternity on paternal investment depends on the relative shapes of the cost and benefit curves, that is, on the effects of the level of paternal investment on offspring fitness and on reproductive success from activities other than paternal effort (see also Houston 1995). As a result, reduced paternity might have a significant effect on paternal investment in some species, but not in others. Unfortunately, we do not know the shapes of the cost/benefit curves and, therefore, we cannot accurately predict what the change in optimal paternal effort would be for a given change in (certainty of) paternity. We can only discuss the importance of certain costs/benefits in relation to life-history aspects of both species. For example, Wheelwright et al. (1991) manipulated brood size in tree swallows, but could not find any effect on the parents' future reproductive success, suggesting that the cost of feeding offspring is low. If this is the case, and if males have few other possibilities to father offspring within a season, then feeding at the current nest might be the best option available.

The male-removal experiment that had a clear effect on male investment in polyandrous dunlocks did not have any effect on males in monogamous pairs. Davies et al. (1992) suggested that monogamous males could not afford to reduce their parental effort because the total investment in the brood would be lowered (females compensated only partially for the loss of male help), resulting in reduced offspring fitness overall. In contrast, one of the two males in a polyandrous group could reduce his parental effort because the remaining male plus the female were still available to provide full care.

A reduction in male investment affects offspring fitness in many socially monogamous species (Bart & Tornes 1989). There is clear evidence that the absence of the male strongly affects reproductive success in our populations of tree swallows (Leffelaar & Robertson 1986, see also Dunn & Robertson 1992) and eastern bluebirds (Meek & Robertson 1994b). Under these circumstances, the benefits of reducing investment are perhaps unlikely to outweigh the costs of reduced success of the current brood, assuming that at least some of the offspring are within-pair. Eastern bluebirds usually produce second broods, so males can trade off investment in the first and the second brood. However, we do not know whether males can increase their parentage in the second brood.

Yezerinac et al. (1996) used a similar argument to explain the absence of a relationship between paternity and paternal care in the yellow warbler, *Dendroica petechia*; they showed that males that re-nested either did not change their paternity or their paternity was reduced. From the above, we can predict that males will be more likely to reduce their investment in relation to their paternity in species or in populations where their help is less important for offspring fitness (see Gowaty 1983 for an example of a population of eastern bluebirds where the absence of male care did not affect reproductive success).

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