Male reed buntings do not adjust parental effort in relation to extrapair paternity

Karen M. Bouwman, a C(Kate). M. Lessells, b and Jan Komdeur a

Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, the Netherlands and Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 40, 6666 ZG Heteren, the Netherlands

Parental effort is considered to be costly; therefore, males are expected to provide less care to unrelated offspring. Theoretical models suggest that males should either reduce their care to the entire brood or alternatively distinguish between related and unrelated nestlings and direct provisioning to kin when paternity is in doubt. Reed buntings (Emberiza schoeniclus) have been found to have high levels of extrapair paternity (EPP, i.e., offspring of a male other than the male attending the nest; 55% of offspring), and males are therefore under strong selection pressure to adjust their parental effort according to the proportion of EPP in their brood. In this study, we investigated whether male reed buntings exhibit a reduction in paternal care (incubation and provisioning nestlings) in relation to decreased paternity. We also assess whether males bias their provisioning toward kin. We measured incubation time, provisioning rates, and food allocation to individual nestlings using video recordings at the nests. Microsatellite DNA analysis was used to analyze the paternity of offspring. In direct contrast to a previous study on the same species, our results provided no indication that males lowered their effort with decreased paternity. Furthermore, in nests of mixed paternity, males did not bias their provisioning behavior to kin. It remains to be investigated whether the absence of a relationship between paternity and paternal care can be ascribed to absence of reliable paternity cues or whether the benefits of reducing paternal care did not outweigh the costs in our study population. We found no evidence that the level of paternal care affected male survival or offspring mass, suggesting that both the benefits and costs of any reduction in paternal care would have been low. Key words: Emberiza schoeniclus, extrapair paternity, kin recognition, parental care. [Behav Ecol 16:499–506 (2005)]

Social monogamy is the most common mating system in birds, and both sexes of the breeding pair are often involved in providing parental care at different stages of the breeding cycle (Lack, 1968; Silver et al., 1985). However, molecular paternity analysis has shown that extrapair paternity (EPP; i.e., offspring of a male other than the male attending the nest) is a widespread phenomenon in birds (Birkhead and Møller, 1992; Griffith et al., 2002; Westneat et al., 1990). As parental effort is considered to be costly (Williams, 1966), males are expected to provide less care to offspring sired by other males (Trivers, 1972).

Theoretical models developed to show how males should alter their parental effort when paternity is in doubt, predict three main outcomes. Early models, which assume that paternity is, on average, the same for all matings, that there is no paternity assessment, and that the only cost of paternal care is missed opportunities of remating (Grafen, 1980; Maynard Smith, 1978), indicated that paternal effort may scarcely or not at all be affected by paternity. After adjusting the assumptions, for instance by giving males the capability of assessing their paternity, other theoretical studies predict that males should reduce paternal care to the brood when the certainty of paternity is low (Westneat and Sherman, 1993; Whittingham et al., 1992; Xia, 1992). Finally, some studies predict that EPP may not only affect total paternal effort but also the allocation of care among individual offspring, such that males discriminate against nonkin (Johnstone, 1997; Westneat and Sherman, 1993).

The adjustment of paternal effort in relation to paternity in an entire brood has been studied in many species (Whittingham and Dunn, 2001). Several studies found no adjustment of paternal effort with decreased paternity (e.g., Dickinson, 2003; Kempenaers et al., 1998; Peterson et al., 2001; Westneat, 1995; Whittingham and Lifjeld, 1995; Whittingham et al., 1993), while others have supported the prediction (e.g., Burke et al., 1989; Lifjeld et al., 1998; Neff, 2003; Neff and Gross, 2001; Sheldon and Ellegren, 1998). For instance, in the reed bunting, Emberiza schoeniclus, when comparing two broods, in the same season, from the same male, but with different proportions of EPP, high proportions of EPP resulted in lower provisioning rates by the territory male (Dixon et al., 1994).

Only two studies have looked specifically at food allocation to individual nestlings in broods of mixed paternity; one on red-winged blackbirds, Agelaius phoeniceus (Westneat et al., 1995) and one on the common yellowthroat, Geothlypis trichas (Peterson et al., 2001). Both studies failed to show that males biased their provisioning behavior toward genetic offspring compared to extrapair offspring. Given the observed level of EPP in both species (red-winged blackbird: 25% of offspring [Westneat, 1995]; common yellowthroat: 20% of offspring [Peterson et al., 2001]), selection pressures may not have been strong enough to develop adjustment of provisioning toward own kin in these species (Johnstone, 1997). For that reason, paternal adjustment toward kin in mixed broods should be studied in a species with higher levels of extrapair paternity.

Reed buntings are an excellent species in which to address the question of whether males distinguish between kin and nonkin. They have levels of EPP—55% of nestlings in 86% of nests (Dixon et al., 1994)—that are among the highest found in socially monogamous passerines (Griffith et al., 2002). They usually form socially monogamous pairs with biparental care during incubating and provisioning and are capable of raising two broods in a single season (O’Malley, 1995), and
males have been shown to adjust their provisioning rate as a function of their paternity level (Dixon et al., 1994). In order to test the generality of behaviors, it is important to compare populations of the same species (Griffith et al., 2005). The present study first investigates whether male reed buntings reduce paternal care (incubation and provisioning) in relation to the proportion of EPP in their broods in a population in the Netherlands, as has been shown previously for provisioning rates in a population in England (Dixon et al., 1994). If paternity levels are comparable between the two populations, then parental behavior is expected to show a similar response to paternity. Furthermore, possible costs and benefits of reducing paternal care are addressed. Second, this study investigates whether males discriminate between kin and nonkin when allocating food to individual nestlings.

METHODS

Data collection

The reed bunting is a small (males: 19 g; females: 17 g), sexually dimorphic passerine. Monogamy with biparental care is the main mating system, but polygamy does occur. The breeding season lasts from mid-April until August. Pairs are capable of raising more than one successful brood per year, and females quickly renest if a brood is predated. Nests are built on or just above the ground. Approximately half of the breeding adults return in subsequent breeding seasons and show high site fidelity (Gramp and Perrins, 1994; O’Mallely, 1995).

In 2001 and 2002, a population of reed buntings was studied in a 13-ha study site, on the island of Noorderplaat (45 ha) in the National Park “De Biesbosch” in the Netherlands (51°45’ N, 4°45’ E). The study site had an average density of 2.5 pairs per hectare. Vegetation consisted of a combination of reeds (Phragmites australis), soft rush (Juncus effusus), hard rush (Juncus inflexus), and various species of grass. The height of the vegetation varied from 50 to 300 cm, with most of the vegetation less than 150 cm. A grid of which each cell was approximately 20 x 40 m was laid across the area for mapping territories and nests.

Within our study site, adult reed buntings were caught using mist nets. Birds were ringed with a numbered aluminum ring and a specific combination of three-color rings for individual recognition. A blood sample (20 µl) was taken from the brachial vein and stored in 96% ethanol at room temperature. Nests were located through systematic searches that flushed females off the nest or through checking territories for any nest-related activities. To minimize the risk of predation, which was mainly by stoats, Mustela erminea, and polecats, Mustela putorius, nest visits were kept to a minimum. Nestlings were blood sampled 2 days after hatching by taking a small blood sample (10 µl) from the leg vein.

In both years, video recordings during incubation and provisioning stage were made between 5 May and 19 July and spread over the day between 0700 and 1900 h. No recordings were made during rainfall. Video recordings of the provisioning stage were limited to the time period when the first-hatched chick was between 4 and 6 days of age. A dummy camera was placed at the nest a day before the video was made to familiarize the birds with the camera. The actual camera consisted of a color mini camera (model AVC56P/F56, size: 3 x 3 x 2 cm) connected to a Sony video Hi8 camera recorder (model CCD-TR504E) with line-in function, which recorded for 3 h (90-min tape on long play). The camera was placed on a metal wire approximately 30 cm above the nest, giving a clear view of the nest. The Hi8 camera recorder was placed several meters away from the nest behind a bush. After the camera was placed, the adults quickly returned to the nest (4.06 ± 0.45 min, n = 50). Before recording provisioning behavior, the nestlings were weighed and individually marked on their bill, using a nontoxic black marker. The order of the markings was at random, and the sex and paternity of the nestlings were unknown.

Nestlings were weighed again at 7 days of age and given a numbered aluminum ring. This is the latest that offspring can be taken out of the nest without running the risk of premature fledging.

Video analyses

Videos were analyzed using a television (Sony Trinitron) and VCR (Sony SLV-T2000) with real-time display. The total recording time was defined from the time of the first return of one of the parents until the end of the videotape. The time of day, time of season, number of eggs or nestlings in the nest, and age of the first-hatched nestling in days was known for each recording. Video recordings of incubation behavior had an average length of 167 ± 3.27 min (n = 63). Of these nests, 48 survived at least until eggs hatched and nestlings could be blood sampled and hence paternity determined (Table 1). The incubation behavior of 31 different pairs, for which the proportion of EPP in their broods was later determined, was recorded at least once (Table 1). Incubation was expressed as the number of minutes per hour spent incubating. Video recordings of provisioning behavior were made at 58 nests (Table 1), with an average length of 177 ± 1.82 min. The provisioning behavior of 31 different pairs was recorded at least once (Table 1). Provisioning rate was measured as the number of feeds per nestling per hour, for each parent. A nestling was considered fed when it swallowed (part of) a food item; therefore, during one single visit, more than one nestling could receive food. The sex or paternity of the nestlings was unknown when scoring the videotapes.

Sex determination and paternity analysis

DNA was extracted from blood samples using salt extraction (Richardson et al., 2001). Nestlings were sexed using Griffith’s universal polymerase chain reaction (PCR) method for the sexing of birds (Griffiths et al., 1998). The paternity of the nestlings was analyzed using four fluorescently labeled microsatellite markers: Esq1, Esq4, Esq6 (Hanotte et al., 1994), and Pdoq5 (Griffith et al., 1999). PCR amplifications were performed using a Thermolyne amplitron II thermal

<table>
<thead>
<tr>
<th>Year</th>
<th>Total nests</th>
<th>All nests with known paternity</th>
<th>Number of different pairsa</th>
<th>Pairs with double broods</th>
<th>Double broods with ΔEPPb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation</td>
<td>2001</td>
<td>14</td>
<td>6</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>49</td>
<td>42</td>
<td>26</td>
<td>11</td>
</tr>
<tr>
<td>Provisioning</td>
<td>2001</td>
<td>17</td>
<td>7</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>41</td>
<td>39</td>
<td>26</td>
<td>9</td>
</tr>
</tbody>
</table>

a One nest per pair; individuals only included once (i.e., excluding remated individuals and secondary females).

b ΔEPP = difference in proportion of EPP between broods of the same pair.
addition, provisioning effort is expressed as provisioning rate proportion ("share") of male and female effort combined. In Dixon et al. (1994). As pairs remained together and on the relater the difference in proportion of EPP between nests with Pairs that reared two broods in a single season were used to Statistical analysis had a total exclusionary power of 0.978 and 0.996 for the first cycles of 1 min at 94°C, 1 min at annealing temperature, and 1 min at 72°C. Annealing temperatures were set at 55°C for Esq1 and Esq4, at 52°C for Esq6, and 50°C for Pdoq5. Each 10-μl mix contained 10–50 ng of DNA, 1.0 μM of each primer, 0.2 mM of each deoxynucleoside triphosphate, 0.05 units of Taq polymerase (Advanced Biotecnologies, Columbia, MD), and 0.625 mM MgCl₂ in a supplied reaction buffer (final concentration 20 mM (NH₄)₂SO₄, 75 mM Tris–HCl, pH 9.0, 0.01% [w/v] Tween). PCR products were diluted two times. Diluted PCR products of Esq1, Esq4, and Pdoq5 were multiplexed in a ratio of 2:1:2, after which 1 μl of PCR product (Esq6) or multiplex mixture was mixed with 1.5 μl of a loading buffer containing 1.1 μl of deionized formamide, 0.18 μl of blue dextran loading dye, and 0.02 μl of internal lane standard (ROX500, Applied Biosystems, Foster City, CA). These samples were denatured by heating at 94°C for 3 min and then placing directly on ice. One microliter of each sample was electrophoresed using a 10% denaturing polyacrylamide gel on an Advanced Biotecnologies ABI 377 XL DNA sequencer. DNA fragments were analyzed using DNA fragment analysis software (Advanced Biosystems GENESCAN [version 3.1] and GENOTYPER [version 2.5]). Parentage was determined by using a likelihood-based approach in CERVUS (Marshall et al., 1998). This program assesses the confidence of paternity assignment through a simulation based on allele frequencies in the population, the number of possible parent-candidates, and the number of parent-candidates sampled. The male and female present at a nest were determined by observations of color-ringed birds during the incubation and nestling period. Potential offspring of the male and female within the territory were identified using CERVUS. First, potential offspring of each female were identified to check for egg dumping; then, potential offspring of each male were identified using the mother as "known parent" in the analysis. Using a known parent in the analysis increases the confidence level when determining the father. CERVUS was given the evidence that the two broods of a male differ more in the same year, we tested whether there was significant variance between the broods of a male differ more in the proportion of extrapair young than expected by chance if individual nestlings in both broods have the same probability of EPP. In these analyses, the relevant test deviance was the residual deviance after fitting male identity as an explanatory variable in the model. The randomization test was carried out by simultaneously reallocating the paternity of nestlings within each male across his two broods, while maintaining the observed sample size of broods per male or for first and second broods. Third, when we analyzed data for males with two broods in the same year, we tested whether there was significant variance between the first and second broods by fitting male identity or brood number (first or second) as explanatory variables in the model. In the randomization tests, we reallocated the observed proportions of extrapair young in the brood (i.e., the number of extrapair young and the corresponding number of young genotyped) across broods while maintaining the observed sample size of broods per male or for first and second broods. Second, we tested whether there was significant variation in the proportion of extrapair young between males (when we analyzed data for males with two broods in the same year) or between first and second broods by fitting male identity or brood number (first or second) as explanatory variables in the model. In the randomization tests, we reallocated the observed proportions of extrapair young in the brood (i.e., the number of extrapair young and the corresponding number of young genotyped) across broods while maintaining the observed sample size of broods per male or for first and second broods. The randomization test was carried out by simultaneously reallocating the paternity of nestlings within each male across his two broods, while maintaining the observed brood sizes of all broods in the sample. Broods of mixed paternity were used to investigate whether males bias their provisioning toward own kin. This way, no correction is necessary for age of the nestlings. For each brood, the average number of feeds per nestling per hour (provisioning rate) was calculated first for sons and daughters and then for within- and extrapair nestlings. To avoid pseudoreplication, only one nest was included for each pair. If the provisioning behavior of a pair had been recorded on more than one occasion (i.e., from more than one brood in a season), then the brood in which the numbers of within- and extrapair young were most similar was included. Statistical analyses were performed using SPSS 11.0.1 (2001), except for power analysis, which was performed using GPOWER (Erdfelder et al., 1996). All data were tested for
normality, and data that were not normally distributed were transformed to achieve normality, or nonparametric tests were used. Unless stated, means are expressed with standard errors, probability values are two-tailed, and the level of significance was set at $p < .05$.

**RESULTS**

**Breeding ecology**

Low levels of polygamy were found in both years; 9% of ringed males ($n = 11$) in 2001 and 5% of ringed males ($n = 39$) in 2002 had two females on their territory. Male incubation and provisioning behavior at primary nests were within the range of male incubation and provisioning behavior at monogamous nests (Table 2). Polygamous males did not incubate or provision at secondary nests. No difference was found between male provisioning behavior at monogamous and primary nests in this study or in that by Dixon et al. (1994); therefore, no distinction was made in subsequent analyses. Secondary nests of polygamous males are excluded from further analyses.

On average, a clutch consisted of $4.5 \pm 0.07$ eggs ($n = 125$ nests, range 2–6), with a hatching success of 86%. This resulted in broods containing an average of $3.92 \pm 0.11$ nestlings at a higher rate than males (Table 2; Wilcoxon signed-rank test—incubation time: $Z = -4.86, n = 31, p < .001$; provisioning rate: $Z = -3.63, n = 31, p < .001$). Males assisted in incubating eggs in 35% of cases ($n = 31$ males). There was a significant negative correlation between male and female incubation time ($r_{spearman} = -0.82, n = 11, p = .002$). No effect was found of clutch size, time of day, day of incubation, or day of season on the presence or absence of male incubation (logistic regression: all $p > .5, n = 31$), on the time spent incubating by male or female (general linear model [GLM]—males [after log transformation]: all $p > .2, n = 11$; females: all $p > .2, n = 31$), or on the male share of incubation (GLM [after log transformation]: all $p > .8, n = 11$).

The effect of age of nestlings, time of day, day in season, brood size, and provisioning rate of partner on provisioning rate was tested, and a significant relationship was shown to occur between age of nestlings and provisioning rate for both females and males (GLM—females [after log transformation]: age $F_{1,31} = 7.03, p = .01$, brood size $F_{1,31} = 4.03, p = .06$, rest $p > .4$; males: age $F_{1,31} = 12.03, p = .002$, rest $p > .3$). A male’s share of provisioning was not related to age of nestlings, time of day, day in season, or brood size (GLM: all $p > .2, n = 31$).

**EPP**

In total, 294 nestlings from 75 nests were genotyped (2001: 38 nestlings from 10 nests, 2002: 256 nestlings from 65 nests). At 63 nests, both male and female members of the breeding pair were caught, and at 12 nests, only the male was caught. No cases of intraspecific brood parasitism were found; all nestlings had genotypes consistent with their being offspring of the female attending the nest, that is, the putative mother, at a 95% confidence level (2001: $n = 19$ nestlings, 2002: $n = 232$ nestlings). The male attending the nest was excluded from being the genetic father at a 95% confidence level for 49.7% of nestlings; thus, these nestlings were sired by an extrapair male (2001: 18/38 nestlings versus 2002: 128/256 nestlings; $\chi^2 = 0.017, df = 1, p = .90$). On average, 80.0% of nestlings contained at least one extrapair young (2001: 6/10 nestlings versus 2002: 54/65 nestlings). A male’s paternity in 22.7% of nests (2001: 4/10 nests, 2002: 13/65 nests), that is, all offspring were extrapair. Absolute differences in proportion of EPP between first and second nests of the same pair ranged from 0 to 0.75 (Table 3). Among the broods produced by 21 pairs for whom two broods produced in the same year were genotyped, the proportion of extrapair young in a brood varied significantly between the 42 broods in the sample (deviance = 81.89, df = 41, $p$ [randomization test] = .003). However, individual males did not differ in the proportion of extrapair young in their broods (change in deviance = 40.04, df = 20, $p$ [randomization test] = .82). Neither did first broods differ systematically from second broods in the proportion of extrapair young (average percentage of EPP nest 1 and nest 2: 51% and 56%; change in deviance = 0.70, df = 1, $p$ [randomization test] = .48). Nevertheless, there was a significant variation between broods within males (residual deviance = 41.86, df = 21, $p$ [randomization test] = .029). This shows that the probability of a nestling having EPP differs between the broods produced by a single male in the same year.

**Paternity and parental care**

Care toward entire broods

Incubation observations and EPP levels were available for 12 pairs (consisting of the same partners remaining on the same territory) that produced two clutches in a single season (Table 1).
Eleven of these pairs had numerically different proportions of EPP in their first and second broods; overall, for the 12 pairs, there was a statistically significant variation between the two broods within-pairs (residual deviance = 25.95, df = 12, \( p \) [randomization test] = .040). We found no relationship between the difference in proportion of EPP between broods and the difference in male share of incubation (Figure 1a). Provisioning observations were available for 10 pairs that raised more than one brood in a season (Table 1). Proportions of EPP differed numerically between the first and second broods in nine of these pairs; overall, for the 10 pairs, there was a statistically significant variation between the two broods within the pairs (residual deviance = 22.61, df = 10, \( p \) [randomization test] = .013). No relationship was found between difference in proportion of EPP and difference in male share of provisioning (Figure 1b) or difference in maternal and paternal provisioning rates per hour per nestling (Figure 1c,d) corrected for nestling age. Although the sample size is small, the power analysis showed that a significant relationship similar to the one in Dixon et al. (1994) would have been detected with a probability of \( p > .85 \) for \( z = 0.05 \) \( (r = .75, \text{ critical } t_{0.05} = 2.31, n = 10) \). Males incubated at four nests and provisioned at eight nests where they had no paternity at all. There were no differences in male share of both incubation and provisioning between nests with no EPP and nests with at least one extrapair offspring (Mann-Whitney \( U \) test—incubation: \( U = 81.0, n_{\text{no EPP}} = 8, n_{\text{EPP}} = 23, p = .59 \); provisioning: \( U = 72.5, n_{\text{no EPP}} = 6, n_{\text{EPP}} = 25, p = .90 \)). Furthermore, there was no relationship between male share of incubation and provisioning and the proportion of EPP in the brood among all males (incubation: \( r = -.022, n = 31, p = .91 \); provisioning: \( r = .16, n = 31, p = .38 \)).

**Costs and benefits of paternal care**

Nestlings of 33 nests were weighed before fledging. In one nest, some nestlings died before 7 days of age and were therefore excluded from the analysis. No relationship was found between the number of nestlings in the nest and the average mass of nestlings at day seven \( (r = .15, n = 32, p = .40) \). Furthermore, there was no correlation between male provisioning rate and average fledging mass (provisioning rate corrected for nestling age; \( r = .04, n = 32, p = .83 \)). A negative trend was found between female provisioning rate and average fledging mass (provisioning rate corrected for nestling age; \( r = -.32, n = 32, p = .07 \)). Total provisioning rate showed no relationship with average fledging mass (provisioning rate corrected for nestling age; \( r = .17, n = 32, p = .36 \)).

Male total parental effort was estimated by adding together a male’s share of incubation and provisioning. There was no relation between male total parental effort and his survival to the next year \( (U = 53.5, n_{\text{dead}} = 9, n_{\text{survive}} = 16, p = .30) \).

**Food provisioning to within- and extrapair young**

Video observations of provisioning behavior where the allocation of food to individual nestlings of mixed sex could be observed were made at the nests of 30 different males. Neither males nor females biased provisioning to either sons or daughters (Wilcoxon—males: \( Z = -0.412, p = .68, n = 30 \); females: \( Z = -0.738, p = .46, n = 30 \)). Therefore, no distinction was made in subsequent analysis. Recordings were available for nests belonging to 20 different males, containing nestlings of mixed paternity. At the time of observation, extrapair young had similar mass as within-pair young when correcting for age (GLMM: \( \chi^2 = 0.027, p = .87, n = 88 \)).
Behavioral Ecology

females: mixed paternity (Wilcoxon—males: [Sheldon et al., 1997]. It has not yet been investigated which

2000; Møller, 1988), and absence of female during egg laying

1992), frequency of extrapair copulations (Ewen and Armstrong,

investment in relation to paternity, it is important to know

paternity levels between nests of the same male in the same

success in another brood. Several studies have shown varying

levels of paternity between nests of the same male (e.g., Dunn

et al., 1994; Yezerinac et al., 1996); in two different popu-

lations of reed buntings significant variation was found in

paternity levels between nests of the same male in the same

season (Dixon et al., 1994; Lessells, 1994; this study).

Second, males should be able to assess their share of

paternity. The actual level of paternity in broods can be

measured relatively easily using molecular techniques; how-

ever, the certainty of paternity from a male point of view

cannot be measured (Kempenaers and Sheldon, 1997).

different studies trying to experimentally decrease certainty

of paternity generated different results, as some did (Sheldon

and Ellegren, 1998) and others did not (Kempenaers et al.,

1998) find a decrease in paternal care. In the latter case, it is

not possible to determine whether the certainty of paternity

was not decreased by the experiment or whether there was no

response in paternal care to the successfully manipulated

certainty of paternity (Wright, 1998). When studying paternal

investment in relation to paternity, it is important to know

whether paternity cues are available, as no adjustment of

paternal care can be expected if males cannot assess their

paternity (Whittingham and Dunn, 2001). In other species,

males have been shown to judge their share of paternity using

access to the female during her fertile period (Davies et al.,

2000; Møller, 1988), and absence of female during egg laying

(Sheeldon et al., 1997). It has not yet been investigated which

cues reed bunting males use to assess their paternity;

therefore, it remains unknown whether this assumption is

actually met. As a significant variation was found in levels of

paternity between broods of the same male, information may

be available from which males can derive their certainty of

paternity (Lessells, 1994). Male reed buntings guard their

mates during the fertile period, but only part-time, and both

males and females were often seen to leave their territory, for

example, to forage. Males were often seen intruding into a

fertile female’s territory. However, due to the secretive

behavior of females, we do not know whether females also

make forays into other territories in search of extrapair males.

Intruding males were usually chased by the territorial male, if

he was present, while the female seemingly did not pay any

attention. We never witnessed extrapair copulations. Thus,

possible cues may be (1) absence of the female during her

fertile period, (2) the number of intruding males into the
territory, or (3) how the female reacts to these males.

Third, the benefits of reducing paternal care should

outweigh the costs. The benefits of reducing care for the

mate, in most cases, can be decreased mortality (Nur, 1984; Yezerinac et al.,

1996) and/or increased opportunities for additional matings

(Magrath and Elgar, 1997; Smith, 1995; reviewed in Magrath

and Komdeur, 2003). The costs of reducing parental care

seem obvious in terms of decreased survival of offspring (Bart

and Tornes, 1989; Wolf et al., 1988). Monogamous males may

not be able to afford to reduce parental effort, as all offspring

would suffer, including a male’s own offspring (Davies et al.,

1992). This would, however, not be the case if males can
distinguish between related and unrelated offspring and

provide more care toward kin. In the present study, no
evidence of benefits or costs of reducing care was found.

Males did not appear to benefit through decreased mortality

when providing less paternal care. Neither was there any

relationship detected between fledging mass and male

provisioning rate. Possibly, our measure of paternal care is

not a good representation of paternal investment, thereby

failing to show an effect. Potentially, when providing less care,

males may gain a reproductive benefit through increased

extrapair fertilizations. These can occur throughout the

breeding cycle as reed buntings breed asynchronously and

are multibrooded. More needs to be known about the effect

of paternal effort on offspring fitness and on a male’s

reproductive success resulting from other activities than

parental care, such as extrapair mating behavior, to ade-
quately address the third theoretical requirement.

Male reed buntings in an English population have been

shown to decrease their provisioning rates when their

paternity is reduced (Dixon et al., 1994). The change in

provisioning is, however, very marginal: when paternity is

reduced by 100% from one nest to the next—a change greater

than expected from binomial variation (Lessells, 1994)—

provisioning rates only decrease by approximately 0.1 feed per

nestling per hour. This would be a change of 4%, when

comparing this to an average provisioning rate of 26 feeds

per hour per nestling (Dixon, 1993). Females do not show any

compensation for the decrease in male provisioning rates,
possibly because the decrease is very small. As male reed

buntings provide care even when they have no paternity in

the brood, they may be prone to making large paternity

assessment errors.

The absence of a relationship between paternity and

paternal care may be due to the absence of reliable cues to

assess paternity or to benefits of reducing care not exceeding

costs (Whittingham and Dunn, 2001). The reason why males

differed in their provisioning behavior as a function of their

paternity levels between the populations in England and the

Netherlands remains unclear. The sample size in our study
Food provisioning to within- and extrapair young

In the absence of a relationship between paternity and overall paternal care in the reed bunting, discrimination against nonkin may still occur. As female reed buntings are related to all the offspring in the nest, they are not expected to bias their provisioning behavior (as shown in our results). However, males do experience high levels of cuckoldry but fail to show any bias when allocating food to individual nestlings. In addition, males have been observed to provision at nests in which they had no paternity at all (Burke et al., 1989; Dixon et al., 1994; this study). Furthermore, no relationship was found between paternal effort and male survival to the following breeding season and between male provisioning rate and fledging mass of nestlings. Therefore, the costs for a male to provision to unrelated offspring or the benefits for related offspring to be recognized as kin by the father may not be high enough to generate kin discrimination (Johnstone, 1997). This study confirms previous studies of a lack of kin recognition in parental care (reviewed by Kempenaers and Sheldon, 1996).

To conclude, this study found no indication that male reed buntings decreased their paternal effort in relation to paternity, both between nests of the same male in one season and between individual nestlings. The availability of cues to assess paternity and costs and benefits of reducing care, which are often neglected (Yezerinac et al., 1996), play a crucial role in the relationship between paternity and paternal care. This study included two aspects of costs and benefits of reducing care, namely, fledging mass and male survival in relation to paternal effort; however, other aspects (e.g., fledging survival and recruitment, male extrapair fertilization success) also need to be addressed to understand the trade-off between paternal care and other activities (such as self-maintenance or extrapair mating behavior). Furthermore, the need to study more than one population per species is stressed, as local circumstances may play an important role in variability in paternal care in relation to paternity.

We thank Suzette Flantua, Leonie Rijmakers, and Carmen van der Veen for help in the field and Jan Wijmenga, René van Dijk, and Cas Eikenaar for help both in the field and with analyzing the videos. We also thank Terry Burke for giving us the opportunity to do part of the paternity analysis at the Sheffield Molecular Genetics Facility. We are grateful to Staatsbosbeheer, who allowed us to work and live in “De Biesbosch,” and especially to Dick Feij and Bart Weel, who arranged the practicalities. The manuscript benefited from constructive comments by Rudi Drent, Cas Eikenaar, David Richardson, and two anonymous referees. Financial support was provided by NWO to J.K. (805-344005) and Schure-Beijerink-Popping Fund of KNAW to K.B. (SBP/JK/2003-30).

REFERENCES


Food provisioning to within- and extrapair young

In the absence of a relationship between paternity and overall paternal care in the reed bunting, discrimination against nonkin may still occur. As female reed buntings are related to all the offspring in the nest, they are not expected to bias their provisioning behavior (as shown in our results). However, males do experience high levels of cuckoldry but fail to show any bias when allocating food to individual nestlings. In addition, males have been observed to provision at nests in which they had no paternity at all (Burke et al., 1989; Dixon et al., 1994; this study). Furthermore, no relationship was found between paternal effort and male survival to the following breeding season and between male provisioning rate and fledging mass of nestlings. Therefore, the costs for a male to provision to unrelated offspring or the benefits for related offspring to be recognized as kin by the father may not be high enough to generate kin discrimination (Johnstone, 1997). This study confirms previous studies of a lack of kin recognition in parental care (reviewed by Kempenaers and Sheldon, 1996).

To conclude, this study found no indication that male reed buntings decreased their paternal effort in relation to paternity, both between nests of the same male in one season and between individual nestlings. The availability of cues to assess paternity and costs and benefits of reducing care, which are often neglected (Yezerinac et al., 1996), play a crucial role in the relationship between paternity and paternal care. This study included two aspects of costs and benefits of reducing care, namely, fledging mass and male survival in relation to paternal effort; however, other aspects (e.g., fledging survival and recruitment, male extrapair fertilization success) also need to be addressed to understand the trade-off between paternal care and other activities (such as self-maintenance or extrapair mating behavior). Furthermore, the need to study more than one population per species is stressed, as local circumstances may play an important role in variability in paternal care in relation to paternity.

We thank Suzette Flantua, Leonie Rijmakers, and Carmen van der Veen for help in the field and Jan Wijmenga, René van Dijk, and Cas Eikenaar for help both in the field and with analyzing the videos. We also thank Terry Burke for giving us the opportunity to do part of the paternity analysis at the Sheffield Molecular Genetics Facility. We are grateful to Staatsbosbeheer, who allowed us to work and live in “De Biesbosch,” and especially to Dick Feij and Bart Weel, who arranged the practicalities. The manuscript benefited from constructive comments by Rudi Drent, Cas Eikenaar, David Richardson, and two anonymous referees. Financial support was provided by NWO to J.K. (805-344005) and Schure-Beijerink-Popping Fund of KNAW to K.B. (SBP/JK/2003-30).

REFERENCES
