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ORIGINAL PAPER

Nest desertion is not predicted by cuckoldry in the Eurasian penduline tit

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Abstract Engagement in extra-pair copulations is an example of the abundant conflicting interests between males and females over reproduction. Potential benefits for females and the risk of cuckoldry for males are expected to have important implications on the evolution of parental care. However, whether parents adjust parental care in response to parentage remains unclear. In Eurasian penduline tits *Remiz pendulinus*, which are small polygamous songbirds, parental care is carried out either by the male or by the female. In addition, one third of clutches is deserted by both male and female. Desertion takes place during the egg-laying phase. Using genotypes of nine microsatellite loci of 443 offspring and 211 adults, we test whether extra-pair paternity predicts parental care. We expect males to be more likely to desert cuckolded broods, whereas we expect females, if they obtain benefits from having multiple sires, to be more likely to care for broods with multiple paternity. Our results suggest that parental care is not adjusted to parentage on an ecological timescale. Furthermore, we found that male attractiveness does not predict cuckoldry, and we found no evidence for indirect benefits for females (i.e., increased growth rates or heterozygosity of extra-pair offspring). We argue that male Eurasian penduline tits may not be able to assess the risk of cuckoldry; thus, a direct association with parental care is unlikely to evolve. However, timing of desertion (i.e., when to desert during the egg-laying phase) may be influenced by the risk of cuckoldry. Future work applying extensive gene sequencing and quantitative genetics is likely to further our understanding of how selection may influence the association between parentage and parental care.

Keywords Parental care · Extra-pair copulation · Indirect benefits · Breeding system · Penduline tit · *Remiz pendulinus*

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Introduction

In many species, parental care is crucial for the development and survival of offspring (Lack 1968; Clutton-Brock 1991; Reguera and Gomendio 1999; Gubernick and Teferi 2000; McGraw et al. 2010). Yet the costs of parental care may impair the reproductive output and survival of the parents, underlying a conflict between current investment in care and future reproduction (Williams 1966; Reguera and

Gomendio 1999). As a result, the optimal amount of care provided is different between offspring and parents (parent–offspring conflict; Trivers 1974; Parker and Macnair 1979) and between male and female parents (sexual conflict; Trivers 1972; Parker 1979). Sexual conflict about parental care often results in parents trying to shift the workload of parental care towards each other (Houston et al. 2005; van Dijk and Székely 2008). This may ultimately lead to one of the parents deserting the mate and offspring (Houston and Davies 1985; McNamara et al. 1999). How such conflict is resolved depends on the costs and benefits of caring or deserting. One important variable influencing these costs and benefits is the proportion of offspring sired by the social parents providing parental care (i.e., the genetic share that the parents hold in their offspring). In internally fertilizing organisms, males may be cuckolded (i.e., lose in their genetic share). In that case, males are likely better off investing less in the offspring and saving resources for future reproduction. Females, on the other hand, may benefit from having multiple sires and may thus benefit from investing more in the offspring (Trivers 1972; Queller 1997; Magrath and Komdeur 2003; Kokko and Jennions 2008).

The occurrence of extra-pair offspring has been shown to be an abundant phenomenon among various taxa: in birds, extra-pair paternity (EPP) was reported in 90% of species investigated (Griffith et al. 2004); in nonavian reptiles, EPP was reported in 100% of species investigated (Uller and Olsson 2008); in fish, about one third of nests cuckolded to some extent (DeWoody and Avise 2000); and in mammals, extra-pair offspring was relatively common, with multimale mating occurring in at least 133 species (Wolff and Macdonald 2004). The costs and benefits of cuckoldry have been investigated extensively. Nevertheless, the question on whether parents should, or are able to, adjust their parental effort with the genetic share they hold in the offspring remains largely unanswered (Sheldon 2002; Eliassen and Kokko 2008). Although some studies find support for adjustment of parental care as a response to parentage (Dixon et al. 1994; Lifjeld et al. 1998; Sheldon and Ellegren 1998; Neff and Gross 2001), including studies in humans (Alvergne et al. 2009), such a response may be different between species or populations (Wagner et al. 1996; Dickinson 2003). In the reed bunting *Emberiza schoeniclus*, for instance, it was found that paternal care was negatively associated with the degree of EPP (Dixon et al. 1994; Suter et al. 2009). A different study investigating the same species in a different population, however, found no significant association (Bouwman et al. 2005). Local conditions may influence the ability to assess the risk of cuckoldry and may drive the costs and benefits of parental care (Whittingham and Dunn 2001; Bouwman et al. 2005).

The assessed risk of being cuckolded is possibly more likely to influence subsequent paternal care than the actual occurrence of extra-pair young (EPY) because, at least in some taxa such as birds, the offspring (eggs for instance) may not provide sufficient information for recognition (Davies 1992; Osorio-Beristain and Drummond 2001; Komdeur et al. 2007; Griffith et al. 2009). Perhaps the most direct example of that is provided by interspecific brood parasites such as cuckoos. Although the hosts of these brood parasites will care for the nonrelated offspring when parasitic offspring cannot be recognized, the hosts are more likely to reject the parasitic offspring when parasitism has been recognized. Hosts are also more likely to reject parasitic offspring when the risk is too high (Stokke et al. 2008; Langmore et al. 2009). Similarly, male dunnocks *Prunella modularis* are less likely to provide paternal care as mate guarding becomes more difficult and, therefore, the risk of cuckoldry increases (Davies 1992). Male blue-footed boobies *Sula nebouxii* expelled the eggs from their nest when the risk of cuckoldry was experimentally elevated (Osorio-Beristain and Drummond 2001).

Here we combined detailed field data with paternity analysis using polymorphic microsatellite markers and address whether parents adjust parental care in response to certainty over parentage in Eurasian penduline tits, *Remiz pendulinus*. Penduline tits are uniquely suitable for investigating this question given that either the male parent, the female parent, or both parents may desert the nest in the egg-laying phase, leaving the partner to provide all parental care. Once the female has deserted, the male may start caring for the offspring (in 7–18% of nests). Likewise, once the male has deserted (in 45–65% of nests), the female often starts caring, but only after she has laid two to three more eggs (Persson and Öhrström 1989; van Dijk et al. 2007). Additionally, no less than 28–44% of nests is deserted by both parents (n=16–140 clutches studied in different populations in Europe; Persson and Öhrström 1989; Franz 1991; van Dijk et al., Behaviour, in press). Both males and females may mate multiply and obtain up to six mates in a given breeding season (Szentirmai et al. 2007; van Dijk 2009), while pairs rarely produce multiple clutches together at different nests (van Dijk 2009; van Dijk et al. 2007). Females are known to care for up to two clutches per season, whereas males, once they have cared for one brood, will not care for a second brood in the same breeding season. More attractive males are more likely to desert (van Dijk 2009), and the time for males to find a new mate decreases with attractiveness (Kingma et al. 2008). The total number of offspring produced in a given breeding season largely depends on the parental care strategy adopted at an individual's first nest in a breeding season (van Dijk 2009). The sex difference in desertion rates in penduline

tits may partly be due to the risk for males to be cuckolded, so that the best interest of males is to secure and fertilize many females instead of investing on parental care (Trivers 1972; Queller 1997; Westneat and Stewart 2003; Kokko and Jennions 2008; also Pogány Á, van Dijk RE, Horváth P, Székely T, Sex differences in care provisioning do not explain female-biased uniparental care in the penduline tit *Remiz pendulinus*, in preparation).

Firstly, we investigated how frequently EPP (the genetic father is different from the social father), quasi-parasitism (the genetic mother is different from the social mother; Wrege and Emlen 1987), and egg dumping or intraspecific brood parasitism (both parents are different from the social pair) occur in our population of penduline tits. Both quasi-parasitism and egg dumping are relatively rare phenomena and have been reported in only 12 of 130 (Griffith et al. 2004) and 20 of 69 (Arnold and Owens 2002) bird species studied, respectively, including penduline tits (Schleicher et al. 1997).

Secondly, if the degree of cuckoldry is influenced by a male's mate-guarding behavior (Parker 1974; Davies 1992; Olsson et al. 1996; Osorio-Beristain and Drummond 2001), then a male that deserts too early, and hence performs no mate guarding, would risk losing paternity in the eggs that the female will lay after he has deserted (Arnqvist and Rowe 2005). We would thus expect that nests deserted by males, but not by females, would contain a larger proportion of EPP than male-care nests or biparentally deserted nests. We would predict the same if males can somehow, for instance through mate guarding or the density of potential extra-pair mates for the female, assess the risk of being cuckolded: with an increased risk of cuckoldry for males, they are less likely to provide care, in which case the percentage of EPP should be lower for male-care nests than for female-care nests. We acknowledge that we are not able to reveal the causality of male desertion for which the egg-laying order needs to be known. The higher levels of EPP in female-care nests compared to male-care nests may be a consequence of female infidelity or the risk for males of being cuckolded before desertion, or it may result from the absence of mate guarding after male desertion. However, we note that we tested for an association of parental care strategy with the occurrence of EPP, for which the prediction in either case is the same: higher levels of EPP in female-care nests. From a female's perspective, we hypothesized that females obtain genetic benefits from obtaining extra-pair fertilizations, such as increased heterozygosity by mating with genetically dissimilar mates (Tregenza and Wedell 2002; Hansson et al. 2004; Richardson et al. 2004) and/or attractiveness of offspring by mating with attractive mates ('good genes' or 'sexy sons'; Weatherhead and Robertson 1979; Hamilton and Zuk 1982; O'Brien and Dawson 2007; Suter et al. 2007; Schmoll et al. 2009). Heterozygosity reflects the individual level of genetic diversity and is often associated with reproductive success (reviewed by Hansson and Westerberg 2002). We predicted therefore that female care will be positively associated with the degree of EPP in the nest.

Finally, with regards to the latter prediction, we note that it is still largely unclear which benefits females may obtain from gaining extra-pair fertilizations (Kempenaers 2007; Mays et al. 2008; Magrath et al. 2009; Schmoll et al. 2009). Here we investigate whether females may benefit by obtaining indirect (genetic) benefits from extra-pair fertilizations (cf. 'good-genes' models) by investigating whether EPY grow faster and/or are more heterozygous than within-pair young (WPY) (Bouwman et al. 2007; Cohas et al. 2007; Suter et al. 2007; Fossøy et al. 2008). Increased heterozygosity is expected to be associated with, for instance, better immune defense (through the major histocompatibility complex–gene complex; Richardson et al. 2005; Kempenaers 2007) and success of mating (genetic compatibility; Kempenaers 2007). Various studies have pointed out that EPY may grow faster, may survive better, or are more heterozygous than WPY (Ilmonen et al. 2009; Mulard et al. 2009), yet no consistent pattern exists in the literature (Kempenaers 2007; Mays et al. 2008; Magrath et al. 2009) and, currently, no unambiguous evidence in support of 'good-genes' models exists. In line with this, we also investigate whether more attractive males (i.e., those that have a larger black facial mask; Pogány and Székely 2007; Kingma et al. 2008) are less likely to be cuckolded than less attractive fathers. If females seek extra-pair copulations to obtain indirect benefits through the offspring, one would expect females to be less likely to do so when mated to attractive males. We note, however, that the indirect benefits will have to be substantial to compensate for reduced male care if the likelihood of male care is associated with the occurrence of cuckoldry (Arnqvist and Kirkpatrick 2005; Szentirmai et al. 2007; but see Eliassen and Kokko 2008). In penduline tits, the costs of male desertion to a female are substantial in terms of reproductive output (Szentirmai et al. 2007; van Dijk 2009).

Methods

Field data were collected during the breeding seasons of 2002–2007 at a 1,321-ha fishpond system (Fehértó) in southern Hungary (46º19′N 20º6′E), where approximately 60–90 males and 45–50 females are known to breed each year (these are the number of banded individuals, biased towards males because females are more difficult to trap than males; Szentirmai et al. 2007). We searched the study area for nest-building males and visited each nest approximately every other day for at least 15 min. We determined which parent attended the nest, the date of nest desertion, the number of eggs (approximately on the eighth day after

incubation had commenced), and the number of nestlings (approximately on the tenth day after hatching of the first egg). The latter is highly correlated to the number of fledglings (van Dijk et al. 2007; Kingma et al. 2008). If a parent was not observed for two consecutive nest checks (in which case the final check lasted for at least 30 min), it was classified as 'deserted.' Fifteen minutes appears to be sufficient to confidentially record the presence of each parent (van Dijk 2009; van Dijk et al. 2007), and none of the parents classified as deserted was resighted at the nest afterwards. We refer to nests only cared for by females as 'female-care' nests and to nests only cared for by males as 'male-care' nests. Standard biometrics of both adults and 10-day-old nestlings were taken (see detailed field methods in our field protocol at http://www.bath.ac.uk/bio-sci/biodiversity-lab/pdfs/PT_%20Field%20Guide_1_2.pdf and in Bleeker et al. 2005; van Dijk et al. 2007; Kingma et al. 2008). All trapped individuals were banded with a numbered metal band from the Hungarian Ornithological Institute, and adults were marked using a unique combination of three colorbands (A.C. Hughes, UK). We also took digital photographs of both sides of the mask of adults (for details, see Kingma et al. 2008).

A small blood sample (about 10 μl) was taken by puncturing the brachial vein of adults and nestlings, which we then stored in an Eppendorf tube containing 1 ml of Queen's lysis buffer (Seutin et al. 1991) at 5°C. Clutches that were deserted by both parents were collected and artificially incubated at 37.5°C for 5 days. If embryo development had started, we collected the embryos.

Molecular analyses

DNA was isolated from the blood and embryo samples using the phenol–chloroform–isoamyl alcohol method (Krokene et al. 1996). Penduline tits were genotyped using nine polymorphic microsatellite markers and their 47 alleles (Mészáros et al. 2008). The combined total exclusionary power of the marker set was 0.967 for the first parent (i.e., exclusion probability of the social father, given that he is not the father and the genotype of the mother is unknown) and 0.998 for the second parent (i.e., exclusion probability of the social father when the genotype of the mother is known; CERVUS version 3.0; Kalinowski et al. 2007). For technical details on polymerase chain reaction and DNA fragment analyses, see Mészáros et al. (2008).

Only individuals with at least five successfully genotyped loci were included in subsequent analyses. The number of loci used varied between individuals; however, for the vast majority (536 of 654 individuals; i.e., 82%), we used nine loci, and for only eight individuals, we used five loci [8.6±0.91 (mean±SD) successfully genotyped loci per individual included in the analyses]. The range of exclusion probabilities for five loci, depending on the variability of loci used, was 0.780–0.894 for the first parent and 0.939–0.979 for the second parent. Exclusion of parentage for the male parent, female parent, or both parents was carried out manually by comparing the genotyped microsatellite loci of the offspring with that of its social parents. Both paternity and maternity were excluded if there were at least three mismatches between the genotypes of the putative father and that of the offspring, and between the genotypes of the social mother and that of the offspring, respectively. Egg dumping was assigned when the genotypes of at least three loci did not match that of either the social father or the social mother (for similar methods, see Magrath et al. 2009; Muck et al. 2009).

Statistical analyses

We used binary logistic regression models to investigate whether the proportion of EPP (i.e., the offspring was not sired by the putative father, but the genotype matched that of the social mother) predicted the parental care strategy (i.e., care or desert) by the male parent, the female parent, or both parents. In addition, we repeated these analyses for the occurrence of EPY (i.e., either the genetic father, the genetic mother, or both are different from the social parents). The latter did not qualitatively change our results (see "Results"). In the analyses with EPY, for males, we pooled EPP and egg dumping, whereas female care was expected to be negatively affected by the occurrence of quasi-parasitism and egg dumping and, hence, these were pooled in the analyses of female-care strategy. In these models, mating date was included to control for a change in parental care strategy over the course of the breeding season. Our data provided an adequate fit to all models (Hosmer–Lemeshow goodness-of-fit: $P>0.331$).

We used linear mixed models (LMMs) with restricted maximum likelihood (LMM) and 10,000 iterations to test for differences in tarsus length, body mass, and heterozygosity between offspring sired by extra-pair males and WPY. Year, parental care strategy (male care, female care, and biparental desertion), sex of the offspring, and level of EPP ('paternity') were included in these models as fixed effects, and brood ID was included as a random effect. The sex of the offspring was, however, only known for the years 2002–2004 (van Dijk et al. 2008). To improve sample sizes, we therefore also present the same LMM, excluding the sex of the offspring. Including a seasonal covariate (mating date) resulted in the convergence not being achieved; thus, this term was not entered into the final LMMs (Table 1). However, brood ID also accounts for potential seasonal variation (e.g., food abundance). We kept the year, parental

Table 1 LMMs comparing the tarsus length and body mass of offspring sired by extra-pair males versus WPY (n=135 broods)

	df	*F*	*P*
Tarsus length			
Year	5	5.394	< 0.001
Parental care strategy	1	6.974	0.009
Paternity	1	0.048	0.826
Body mass			
Year	5	5.725	< 0.001
Parental care strategy	1	4.529	0.035
Paternity	1	0.121	0.728

care strategy, and mating date in the final general linear model (GLM) (Table 2; see "Results").

We analyzed and presented five different indices of heterozygosity, all of which have been previously related to measures of fitness in other species: (1) observed heterozygosity (H_o): the number of heterozygous loci divided by the total number of loci; (2) mean heterozygosity of typed loci (mean H): mean difference in allele length; (3) standardized individual heterozygosity (SIH): observed heterozygosity divided by the mean heterozygosity; (4) mean d^2: the mean squared difference in allele length per locus; (5) standardized mean d^2 (st mean d^2): the mean of the squared difference in allele length divided by the maximum difference per locus, thus weighting for the allele size ranges of the different loci (Coulson et al. 1998; Coltman et al. 1999; Amos et al. 2001; Hansson et al. 2001; Foerster et al. 2003; Bouwman et al. 2007; see Table 3). All indices of heterozygosity were significantly correlated to each other (r>0.376, P<0.001), apart from SIH with H_o, which only showed a significant but weak correlation (r>0.081, P<0.038). We provide the results of all indices here given the variation between the indices and allowing for comparison with previous studies (Foerster et al. 2003; Bouwman et al. 2007). To test for an association between the size of the mask of a male and heterozygosity, we used Pearson product moment correlation for mean H, st mean d^2, and square-root-transformed mean d^2, whereas we used Spearman rank correlation for H_o and SIH. All analyses of heterozygosity were restricted to mixed broods only.

Table 2 GLM testing for the association of percentage of EPP in a brood with brood size (n=113 broods)

Number of nestlings	*df*	*F*	*P*
Year	5	2.745	0.023
Parental care strategy	2	33.121	< 0.001
Mating date	1	11.152	0.001
Paternity	1	1.097	0.297

All analyses were also run using a subsample of those nests where the genotype of both social parents was known. None of those results was qualitatively different from the ones we report here. All statistical analyses were performed in SPSS 17.0 (SPSS, Inc., Chicago, IL, USA). Nonsignificant terms were excluded from the models using stepwise elimination, and we give statistics for excluded variables before their exclusion from the model. Two-tailed probabilities are given, and we rejected the null hypothesis at the P<0.05 level.

Results

We successfully genotyped a total of 443 offspring, 128 adult males, and 83 adult females from a total of 118 nests. Both social parents of 166 (38%) offspring were genotyped, whereas we only genotyped the social father of 199 (45%) offspring and only the social mother of 78 (18%) offspring.

Frequency of EPP, quasi-parasitism, and egg dumping

Of those nests where the genotype of both social parents was known (n_{total}=55 nests), 60.0% of nests (n=33 nests) contained at least one EPY, either through EPP, through quasi-parasitism, or through egg dumping. Among the nests, 52.7% (n=29 nests) contained at least one EPY sired by an extra-pair male, 16.4% (n=9 nests) contained at least one EPY as a result of quasi-parasitism, and 7.3% (n=4 nests) contained at least one EPY as a result of egg dumping.

Out of 166 genotyped offspring where the genotype of both social parents was known, 30.1% (n=50 offspring) was extra-pair: 23.5% (n=39 offspring) was sired by an extra-pair male, 4.2% (n=7) originated from quasi-parasitic females, and genotype did not match with that of either the social mother or the social father for 2.4% (n=4) of offspring. Out of those offspring where we either knew the genotype of both parents or knew only the genotype of the social father (n=365 offspring), 17.0% (n=62) was sired by an extra-pair male. Of those offspring where we only knew the genotype of the social mother, the genotype did not match that of the putative mother in 15.4% (n=12). The latter may be due to either egg dumping or quasi-parasitism.

Extra-pair parentage and parental care

Out of a total of 154 broods included in this study where parental care strategy was known, 18.8% was cared for by the male only, 70.8% was cared for by the female only, and 10.4% was deserted by both parents. The proportion of the young sired by an extra-pair male only (EPP) in a nest did not predict whether the male would care or desert, whether

Table 3 LMMs predicting five different indices of the heterozygosity of offspring sired by extra-pair males versus WPY, restricted to mixed broods only, including and excluding the sex of the offspring as a fixed effect [n=35 broods (119 offspring) and n=45 broods (151 offspring), respectively]

		Including sex of offspring as fixed effect			Excluding sex of offspring as fixed effect		
		df	*F*	*P*	*df*	*F*	*P*
H_o	Year	2	1.084	0.350	4	1.342	0.272
	Paternity	1	0.372	0.543	1	0.042	0.837
	Sex	1	2.836	0.095			
Mean H	Year	2	0.758	0.477	4	1.623	0.185
	Paternity	1	1.217	0.272	1	2.495	0.117
	Sex	1	8.403	0.004			
SIH	Year	2	0.162	0.851	4	0.420	0.793
	Paternity	1	3.459	0.066	1	5.625	0.019
	Sex	1	4.353	0.039			
Mean d^2	Year	2	0.495	0.614	4	1.289	0.288
	Paternity	1	2.939	0.089	1	3.443	0.066
	Sex	1	4.422	0.038			
St mean d^2	Year	2	1.062	0.357	4	1.880	0.129
	Paternity	1	1.142	0.288	1	1.191	0.277
	Sex	1	6.894	0.010			

H_o, observed heterozygosity; mean H, mean heterozygosity; SIH, absolute SIH; mean d^2, mean squared difference in allele length per locus as a measure of the evolutionary similarity of alleles; st mean d^2, standardized mean d^2 (i.e., the mean d^2 divided by the maximum d^2 for a given locus)

the female would care or desert, or whether either the male or the female would care or desert (Table 4, Fig. 1). These results remained unchanged when we replaced EPP with EPY (i.e., EPP, quasi-parasitism, or egg dumping), so that males would be expected to care less frequently when the levels of EPP and egg dumping increased (P=0.746), whereas female care was expected to be negatively affected by the occurrence of quasi-parasitism and egg dumping (P=0.998). The initial models included year as a categorical covariate, but this was excluded from the final binary logistic regression (Table 4) as it did not contribute significantly to these models (P>0.043).

Indirect benefits for females

We found no evidence that offspring sired by extra-pair males grew faster than WPY: there was no difference in tarsus length or body mass between offspring sired by extra-pair males [15.57±1.28 mm and 8.17±1.81 g (n=63 offspring), respectively] and WPY [15.66±1.09 mm (n=342) and 8.33±1.50 g (n=344); Table 1]. Both body mass and tarsus length of the offspring were significantly different across years (Table 1). The sex of the offspring did not contribute significantly to these models (P=0.563 and P=0.314, respectively; n=92 broods) and was thus

Table 4 Binary logistic regression models of male-care and female-care strategies in response to the proportion of EPP (n=114 nests; i.e., all nests where parental care strategy and mating date were known; *df*=1)

Parental care		Model effect estimate±SE	Wald	*P*
Male behavior [care (n=22) vs. desert (n=92)]	Mating date	0.027±0.015	3.245	0.072
	Proportion EPP	0.004±0.008	0.280	0.596
Female behavior [care (n=82) vs. desert (n=32)]	Mating date	− 0.006±0.010	0.278	0.598
	Proportion EPP	0.005±0.008	0.397	0.529
Parent's behavior [care (n=104) vs. desert (n=10)]	Mating date	0.024±0.014	2.867	0.090
	Proportion EPP	0.707±154.719	0.000	0.996

Under 'parent's behavior,' proportion EPP is compared between male-care or female-care nests and those that are biparentally deserted. Separate models were constructed for the parental care behavior (i.e., care or desert) of the male parent, the female parent, and both parents. Sample size n (nests) is given between parentheses for each care strategy. Predicted effect sizes and standard errors are provided.

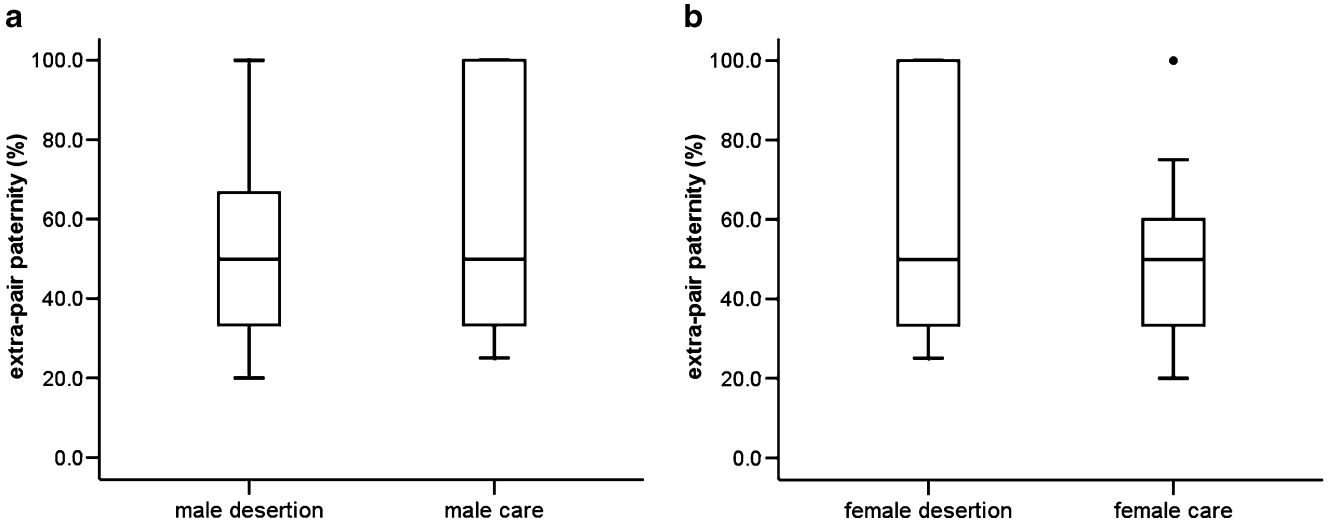

Fig. 1 The association between **a** male-care strategy and **b** female-care strategy and the level of EPP (n=47 broods). Nests containing 0% EPP are excluded from these figures for graphic purposes. See Table 4 for statistics. *Box plots* show the median, interquartile range, outliers, and extreme cases

excluded from the final models presented in Table 1. These results remained unchanged when we restricted the analyses to mixed broods containing both offspring sired by extra-pair males and WPY only (P>0.079). Additionally, parental care strategy was significantly associated with tarsus length (Table 1), so that offspring cared for by females had shorter tarsi than those cared for by males.

The occurrence of EPP was not associated with brood size (i.e., the number of 10-day-old nestlings) (Table 2). Brood size differed significantly across years and declined over the season (Table 2). Parental care strategy predicted the number of nestlings (Table 2), so that brood size at male-care nests or biparentally deserted nests was smaller than brood size at female-care nests.

Parental care strategy did not significantly contribute (P>0.381) to our LMMs testing for a difference in heterozygosity between offspring sired by extra-pair males and WPY, and was thus excluded from the final models. SIH was significantly different between offspring sired by extra-pair males and WPY, so that WPY were more heterozygous than offspring sired by extra-pair males (Table 3). However, none of the other heterozygosity indices was significantly different between offspring sired by extra-pair males and WPY. The nine genotyped loci differed significantly in the length of both alleles (Kruskal–Wallis; χ^2=773.09, P<0.001, n=5,731 differences in allele length), and the standardized mean d^2 did not differ significantly between offspring sired by extra-pair males and WPY (Table 3). Male offspring were significantly more heterozygous than female offspring for mean d^2 and standardized mean d^2, whereas female offspring had a higher mean and SIH (Table 3). None of the sex differences in heterozygosity was significant for the adults (Mann–Whitney U; P>0.076, n=211 adults). Although the sex of the offspring contributed significantly to some of the models in Table 3, it did not qualitatively change the results. None of the heterozygosity indices correlated with the size of the male's mask (P>0.235, n=55 males).

The size of the mask, and hence attractiveness, of a male was not associated with the risk of cuckoldry for a male (i.e., the percentage of EPP in its nest) (GLM; F=0.044, P=0.835, n=62 nests). This GLM included year as a fixed factor (P=0.003), whereas parental care strategy and mating date did not significantly contribute to this model (P>0.149) and were thus excluded from the final model.

Discussion

Consistent with a previous study (Schleicher et al. 1997), we showed that EPP, quasi-parasitism, and egg dumping all occur in the polygamous Eurasian penduline tit, with quasi-parasitism and egg dumping occurring at low frequencies. Yet, the frequency of EPP in our population seems substantially higher: Schleicher et al. (1997) showed that 6.9% of offspring in their study were sired by an extra-pair male, whereas our study suggests an EPP rate of 23.5%. A possible explanation for this discrepancy is the use of different genotyping methods. An alternative explanation is that the frequency of extra-pair copulations may be population specific, with populations possibly varying in, for instance, mate availability, population density, or density of vegetation, which may influence the rate of extra-pair copulations (Davies 1992). However, although the two populations may differ in mate availability, mate guarding appears to be low in both populations (Schleicher

et al. 1997; van Dijk 2009). Additionally, other studies tend to find little difference in the rate of EPP across populations despite various densities, predations rates, or differences in potential female benefits (Krokene and Lifjeld 2000; Conrad et al. 2001; Neff et al. 2008).

Parentage and parental care

The moderate levels of EPP may influence why males would be more likely to desert than females on an evolutionary timescale (Trivers 1972; Queller 1997). Given that the majority (80–95%) of males (Szentirmai et al. 2007; van Dijk et al., Behaviour, in press) desert the offspring, it might seem unlikely that the occurrence of EPP will confound the likelihood of male desertion. However, given that the clutch size of male-care nests is, on average, only about three eggs (van Dijk et al. 2007), the occurrence of only one extra-pair offspring makes up a substantial proportion of the total number of offspring, thus making a male response to cuckoldry potentially adaptive. Our results, however, suggest that parental care in Eurasian penduline tits is not adjusted to parentage on an ecological timescale. This is in contrast with the predicted negative relation between cuckoldry and parental care on an evolutionary timescale (Trivers 1972; Queller 1997), which may partly explain why females desert the nest less frequently than males. This not only furthers our knowledge as to what extent parents should or are able to adjust parental care in response to parentage (Sheldon 2002; van Dijk and Székely 2008) but also has implications for the understanding of which risks parents might face when deciding whether to care for the offspring or to desert. There appears to be little risk for a male by deserting too early after the first eggs have been laid, which may be the reason that males often desert after only three eggs have been laid, leaving the female to finish the nest and clutch. The female often lays two or three more eggs after male desertion. The amount of sperm that can be stored by the female to successfully fertilize those eggs may set the minimum amount of time that a male is 'forced' to stay with its partner to ensure paternity. This remains to be investigated in detail experimentally, yet previous studies have suggested that frequent copulations only act effectively as a paternity assurance prior to or during the early phases of clutch initiation (Crowe et al. 2009; see also 'paternity assurance hypothesis' in Birkhead et al. 1987; Møller 1987). Sperm ejection, however, may pose an important challenge to such paternity assurance (see Peretti and Eberhard 2010).

Given the low levels of mate guarding in this species (Schleicher et al. 1997; van Dijk 2009), the male may not be able to assess the risk of being cuckolded (Davies 1992; Osorio-Beristain and Drummond 2001). Nor does it seem likely that a parent will be able to distinguish between EPY and WPY at the moment that a decision about parental care (i.e., care or desert) is made, which is during the egg-laying phase (Griffith et al. 2009). These may explain why there is no association between the occurrence of EPY in a nest and parental care strategy. Kin recognition may be an important mechanism driving parents to adjust parental care in response to parentage (Alvergne et al. 2009). Yet, the likelihood that this mechanism will work will vary across species and will depend on the developmental stage of the offspring during which parental care is provided (for instance, eggs versus fledged or weaned offspring). Additionally, parental care also often depends on the phenotype of the individual (Lessells 1991). Attractive males may be better at gaining extra-pair copulations (Rhodes et al. 2005; Bouwman et al. 2007; Albrecht et al. 2009) and would thus be better off investing in mating rather than in parental effort, whereas it may pay for less attractive males to invest in parental care (Magrath and Komdeur 2003; Mitchell et al. 2007). This may confound an association between parentage and parental care. However, although attractive males among Eurasian penduline tits are more likely to desert (while females are not more likely to care for the offspring of those males; van Dijk 2009), the risk of being cuckolded was not associated with attractiveness. This also suggests that females may not seek to obtain indirect benefits after male desertion. From a female's perspective, although females mated to less attractive males may seek to obtain indirect benefits through extra-pair fertilizations and are thus more likely to care for the offspring, females mated to attractive males may not need to obtain extra-pair fertilizations. These females are also likely to care for their WPY. This may also obscure an association between the occurrence of EPY and the parental care strategy adopted. Finally, as to whether a male should reduce parental investment in a current brood in relation to the paternity share, the best strategy depends on his future perspectives: if a male is unlikely to enhance its paternity share in future reproduction, he may not be better off reducing investment in the current brood (Houston and McNamara 2002).

Our results are in contrast with the pattern of EPP as observed in blue tits *Cyanistes caeruleus*, where EPP declined markedly with laying order (Magrath et al. 2009). If this would have been true for Eurasian penduline tits as well, then we would expect to find that male-care clutches and biparentally deserted clutches contain a higher proportion of EPY than female-care clutches, given the difference in clutch size between the two. Although this would be counterintuitive given the costs of cuckoldry for males and the potential benefits for females, it would be possible if males would have no cues to detect cuckoldry, such as would be the case with limited mate guarding (Schleicher et al. 1997) or with dense surrounding vegetation (Davies 1992). Alternatively, it is also possible

that the association between the progress of egg laying and paternity differs between species and between clutches. The first eggs laid in clutches later on cared for by females might contain eggs sired by extra-pair males, while this may not be the case for male-care clutches. This possibility deserves further investigation as it may shed light on the causality of nest desertion in relation to EPP. Consistent with our results, Magrath et al. (2009) also suggested that the females' benefits from engaging in extra-pair copulation may need careful reconsideration.

Do females obtain indirect benefits from extra-pair fertilizations?

We did not find strong evidence for indirect benefits that females may gain from obtaining extra-pair copulations: EPY did not grow faster than WPY, nor did EPY appear to survive better from egg to nestling than WPY, as brood size was not predicted by the proportion of EPY in a nest. Also, overall, no difference in heterozygosity existed between EPY and WPY. The current evidence for indirect benefits that females might accrue from obtaining EPP is not unambiguous. Recently, Magrath et al. (2009) showed that the apparent indirect benefits of extra-pair offspring over WPY in blue tits disappeared after controlling for hatching order (see also Arnqvist and Kirkpatrick 2005; Akcay and Roughgarden 2007). Alternatively, fitness benefits for males are often very strong, implying a strong selection pressure for mating multiply, with possible consequences for mating rates in both sexes (Halliday and Arnold 1987; Uller and Olsson 2008; W. Forstmeier, personal communication). In future studies, empirical quantitative genetic data for alternative explanations, but also improved methodology such as more loci or more specifically selected loci, are likely to advance our insight into what the benefits of extra-pair copulations may be for females.

The apparent lack of, or at least limited, indirect benefits from having EPY for female penduline tits may additionally also constrain their interest to obtain extra-pair copulations: if the risk of male desertion increases with increasing proportions of EPY, then the direct costs of male desertion (i.e., lowered reproductive output; Szentirmai et al. 2007) may counterbalance the potential but weak genetic benefits (Arnqvist and Kirkpatrick 2005). As such, selection would be expected to moderate the occurrence of EPY, and an association with the likelihood of caring for or deserting the offspring is then expected to be absent or weak. Nevertheless, although the levels of EPP in Eurasian penduline tits are only moderately high, considering the fact that the pair bond only lasts for about 5 days (van Dijk et al. 2007), it emphasizes the polygamous nature of the species: they enhance their fitness not only by deserting and remating but also through extra-pair copulations during the period that they are together, without incurring the increased risk of being deserted by their partner.

In conclusion, we show that parental care in Eurasian penduline tits is not predicted by moderate levels of cuckoldry and suggest that further studies remain necessary to understand why females engage in extra-pair copulations. For the former, we require more experiments in which (1) the risk of cuckoldry can be assessed (see, for instance, Osorio-Beristain and Drummond 2001), and (2) the extent to which recognition mechanisms may play a role in how parental care depends on the genetic relatedness between parents and offspring can be assessed. Further observational studies investigating to what extent incubation or brood-rearing behavior may be influenced by the occurrence of EPP remain useful for understanding the potential costs to females of reduced male care in response to cuckoldry (see, for instance, Bouwman et al. 2005). To further our understanding of why females obtain extra-pair copulations, we need new approaches, for instance using rapidly advancing molecular techniques. This may include more extensive gene sequencing and application of quantitative genetics to avoid ambiguous results due to loci-specific effects (Masters et al. 2009) and will help to better understand how selection may drive multiple mating in both sexes (Uller and Olsson 2008).

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