



Biparentally deserted offspring are viable in a species with intense sexual conflict over care



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ABSTRACT

Desertion of clutch (or brood) by both parents often leads to breeding failure, since in vast majority of birds care by at least one parent is required for any young to fledge. Recent works in a highly polygamous passerine bird, the Eurasian penduline tit (*Remiz pendulinus*), suggest that biparental clutch desertion is due to intense sexual conflict over care. However, an alternative yet untested hypothesis for biparental desertion is low offspring viability so that the parents abandon the offspring that have poor prospect for survival. Here we test the latter hypothesis in a common garden experiment by comparing the viability of deserted and cared for eggs. We show that embryonic development does not differ between deserted and cared for eggs. Therefore, sexual conflict over care remains the best supported hypothesis for biparental clutch desertion in penduline tits. Our work points out that conflict over care is a potential – yet rarely considered – cause of biparental nest desertion, and a strong alternative for the traditional explanations of low offspring viability, human disturbance or deteriorating ambient environment. Apart from a handful of species, the intensity of sexual conflict has not been quantified, and we call for further studies to consider sexual conflict as a cause of nest desertion.

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1. Introduction

One of the most thoroughly investigated instances of sexual conflict over care decisions is the remarkable breeding system of the Eurasian penduline tit (*Remiz pendulinus*). This small passerine bird is highly polygamous with each sex having up to six mates in a given breeding season (Persson and Öhrström, 1989). In accord, full care of eggs and young is provided by either the female (47% of $N=534$ nests) or male alone (14%); the remaining substantial proportion of nests (39%) are biparentally deserted, dooming these breeding attempts to failure (Pogány et al., 2012). Such care patterns are consistent across five ecologically distant European populations studied to date (Persson and Öhrström, 1989; van Dijk et al., 2010a). Clutch desertion by one or both parents occurs during egg-laying, usually when the clutch contains 3–4 eggs (van Dijk et al., 2007a). In our previous works we reported intense sexual conflict

over parental care in this species, by showing that each sex may increase its reproductive success by deserting and searching for new mates, even though desertion is costly to the mate (Szentirmai et al., 2007; van Dijk et al., 2012 for a comprehensive reference on sexual conflict, see Parker (1979) and Arnqvist and Rowe (2005)). At a given clutch, the outcome of desertion by a parent depends on the mate's decision: offspring are produced only when the mate remains to care, whereas both sexes derive only costs (including time and energy spent on nest-building and egg-production) when the mate also deserts.

Three hypotheses may explain the high frequency of biparental clutch desertion in the penduline tit: sexual conflict over care, uncertain or low parentage, and low offspring viability. First, parents of both sexes can increase their own reproductive success by desertion (Szentirmai et al., 2007), and this strategy should be selected for in a highly polygamous species as long as the lifetime net benefit of care decisions including desertion is higher than caring uniformly. Second, extra-pair offspring may drive desertion (van Dijk et al., 2010b), because large fitness costs are associated with caring for unrelated young, i.e., those sired by extra-pair

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males, or laid by extra-pair females in the nest. Third, low offspring viability may influence biparental clutch desertion to avoid the fitness loss associated with caring for low-quality offspring instead of those with high survival and reproductive prospects. The latter hypothesis follows from the parental investment theory that predicts parental effort to be adjusted to the reproductive value of the current brood (Trivers, 1972). Reproductive value, however, involves two aspects of the current brood: the number and the quality of offspring produced (Fisher, 1930; Williams, 1966), hence we use ‘offspring viability’ to specify that we focus on offspring quality in this study.

To address the offspring viability hypothesis, here we test in a common garden experiment whether deserted and cared for eggs may have different viability. The aim of our study is to test an alternative explanation for biparental desertion in an organism that is frequently used to illustrate sexual conflict over care (Arnqvist and Rowe, 2005; Lessells, 2012; Székely, 2014). Our experiment, however, is important beyond penduline tits for experimentally comparing the viability of naturally deserted and cared for eggs. Low offspring viability is often cited as an explanation for biparental desertion in a wide range of species including seabirds, herons, shorebirds and passerines (Clutton-Brock, 1991; Székely et al., 1996). By comparing the viability and embryonic development between deserted and cared for eggs, we test two predictions: eggs from biparentally deserted nests (i) are less likely to initiate embryonic development than eggs from cared for nests, and (ii) are less likely to reach to an advanced developmental stage.

2. Materials and methods

2.1. Ethics statement

Our research was carried out in the Danube delta (close to Crişan, Tulcea County, Romania, 45°10'N, 29°26'E) with permission from the Danube Delta Biosphere Reserve (reference: 4697/ARBDD/11.03.2010). Ethical guidelines of the association of the study of animal behavior and our home universities were headed. All below research procedures were approved by the Ethical Board of Eötvös Loránd University (reference: ELTE MÁB 02/2014).

2.2. Fieldwork

We monitored the breeding population every other day by searching for new nests, and checking the reproductive stage of established nests (see more details on fieldwork methodology in van Dijk et al. (2007b)). Penduline tits have sexually dimorphic plumage, so adults can be sexed reliably in the field (Pogány and Székely, 2007; Kingma et al., 2008). We trapped penduline tits either using mist nets and song playback before egg-laying (van Dijk et al., 2007b), or inside their nest during incubation by closing the entrance tube. Penduline tits were ringed with a numbered aluminium ring from the Romanian Ornithological Society and a unique combination of three color rings (A C Hughes, Middlesex, UK). Our study aimed to compare the viability of eggs from naturally deserted and cared for nests, and we carefully avoided disturbance-induced desertion in the sensitive period of egg-laying (cf. Valera et al., 1997). Therefore, not all parents were ringed at nests from which we collected eggs for the experiment (both parents ringed at 10.8% of nests, only the male or the female ringed at 35.1% of nests, and neither parents were ringed at 54.1% of $N = 37$ nests, Supplementary Fig. 1). As the identity of several parents was unknown, and the species is highly polygamous, we may have sampled the same individuals more than once. We addressed this possible source of pseudo-replication statistically in a sensitivity analysis. Our results and conclusions did not change after taking into account the possibility of non-independence in our dataset (Supplementary Fig. 2).

Care type and reproductive stage were established by daily observations of attending parent(s), and recording clutch size daily during egg-laying (van Dijk et al., 2007a). Since male-only care is less frequent than female-only care (14% vs. 47%; Pogány et al., 2012; Persson and Öhrström, 1989), we compared biparentally deserted with female-only cared for eggs in this experiment. We collected 78 eggs from 37 nests (18 biparentally deserted and 19 female-only nests). From deserted nests, all eggs were collected (maximum four, with 2.4 ± 0.3 (mean \pm SE) eggs per nest), whereas a maximum of two eggs (with 1.8 ± 0.1 eggs per nest) were collected from cared for nests to avoid disturbance-induced nest desertion. Therefore, number of eggs collected per nest tended to be larger in deserted group than in cared for group (Welch two-sample t -test: $t_{20,8} = 2.0$, $P = 0.057$). Subsequent observations at cared for nests confirmed that the female remained to care following egg-collection at each of these nests. Deserted eggs were collected from inactive nests where no bird was seen at the nest for at least 20 min on two consecutive days (van Dijk et al., 2007a). 2×20 min total observation time is sufficient to assign desertion by the male, the female or both parents in this species, as males and females appear within 3.7 ± 5.2 min (mean \pm SD) and 6.8 ± 7.5 min, (respectively) from start of observation at active nests (van Dijk et al., 2007a). In addition, none of the birds classified as ‘deserted’ based on this method returned to their nests afterwards during any of our field studies to date including this study (e.g., Pogány et al., 2012; van Dijk et al., 2007a, 2010a). Cared for eggs were collected during the course of egg-laying (on day four or five) after male desertion was confirmed (i.e., only the female was present at the nest during two consecutive checks). Therefore, the inactive period (time between the onset of incubation in the incubator and laying of the last egg in a given clutch) was different between deserted and cared for eggs (2.5 ± 0.2 days (mean \pm SE) vs. 0 days, respectively). Eggs are less likely to start embryonic development with increasing inactive period (cf. Arnold et al., 1987). The between-group difference, therefore, may have confounded our analysis of offspring viability and we controlled for the effect of inactive period in the statistical models (see below).

2.3. Incubation of eggs

Eggs were incubated in a purpose-designed incubator (Minimax Keltetőgépek, Vértesszőlős, Hungary), equipped with an automated egg-rotation mechanism. Eggs were marked with a permanent marker based on care type, and eggs from the same nest were placed in the incubator in groups. Temperature was kept automatically at 36.8 ± 0.1 °C, whereas humidity was controlled manually at 60–70%. Humidity was measured two times daily from a digital humidity meter (Boneco 7054 Thermohigrometer, Plaston Group, Widnau, Switzerland) from inside the incubator, and we adjusted humidity by placing more (or fewer) water pots into the incubator to change the area of evaporating water surface. Because we had only one incubator in which new eggs were placed continually during the study, we kept constant temperature and humidity, as well as egg-rotation frequency, which are optimal for early and mid-development of embryos. This method, although optimized from experimental point of view, resulted in sub-optimal conditions during the last few days of embryonic development (cf. Gage and Duerr, 2007) and hence low hatching success.

Eggs were candled twice daily (between 0500 and 0600 h, EEST, and 1900–2000 h) using a LED light to monitor development. Signs of embryonic development becomes apparent by day four, therefore, if no embryo was observed by day six, the egg was removed from the incubator and was considered as not developing. For eggs that started to develop, either the date when embryo development ended or the date of hatching was recorded. In this study, we followed offspring development until hatching, and hatched young

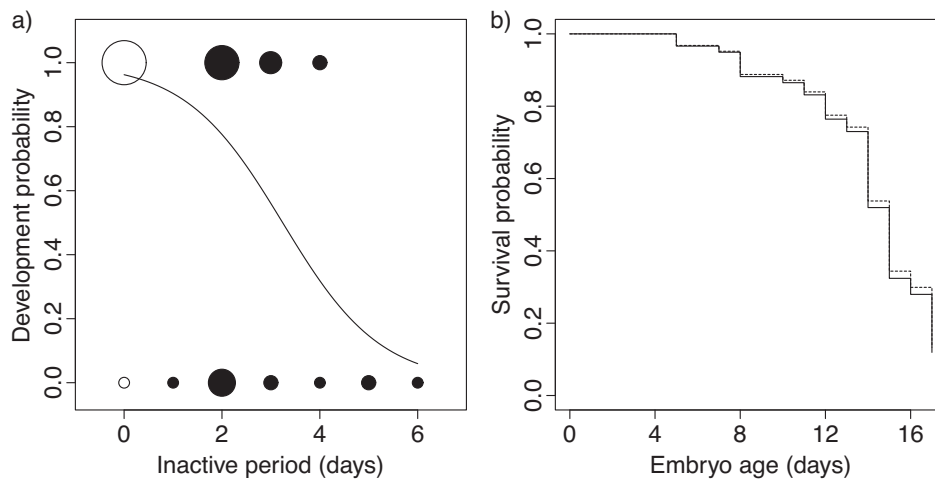


Fig. 1. Offspring viability of artificially incubated eggs collected from biparentally deserted and female-only cared for Eurasian penduline tit nests. (a) Probability of embryonic development of deserted ($N = 43$, filled symbol) and cared for eggs ($N = 35$, open symbol) in relation to the duration of inactive period (i.e., time between onset of incubation in the incubator and laying of the last egg; see Section 2.4. of methods for model details). Symbol diameter is proportional to $(\text{no. of eggs})^{0.4}$, and the solid line gives predictions for the two groups together. (b) Embryo survival in relation to embryo age of deserted ($N = 26$, solid line) and cared for eggs ($N = 34$, dotted line). Embryo survival data includes only eggs that have initiated development.

were returned to nests in the wild population the morning following hatching in the incubator. Young that hatched in the deserted group were fostered to non-experimental nests with similarly aged chicks whereas young that hatched in the cared for group were returned to the nest from which they were collected. The fate of the returned chicks was not followed (for reasons see Section 4.).

2.4. Statistical analyses

We analysed two responses measuring offspring viability, using the R statistical environment (v. 2.15.1, R Development Core Team, 2012). First, start of embryonic development (binary response variable) was analysed using binomial Generalized Linear Mixed Models (GLMM, R package ‘lme4’) with experimental group (factor with two levels: deserted vs. cared for) as a fixed effect and nest ID as a random term.

Second, we analysed the duration of embryonic development in eggs that started to develop. Embryo survival was analysed in Cox Mixed Models (R package ‘coxme’) with duration of development (no. of days surviving) as the response, and end of development as a terminal event. Individuals that hatched were treated as censored observations, and experimental group (fixed effect) and nest ID (random effect) were included as explanatory variables.

The effects of explanatory variables were analysed by likelihood ratio tests in both analyses. Since the inactive period was different between experimental groups (see above), we first checked for its possible confounding effect on the responses, and kept this covariate in the models if it had a significant effect, i.e., included in the analysis of the start of embryonic development (see below), but excluded in the analysis of embryo survival ($P = 0.96$).

Because of the suboptimal conditions for hatching in the incubator the hatching success was lower than in nature (33% as opposed to 73% in nature, the latter based on data collected for Pogány et al. (2012)). Only 8 eggs hatched in the deserted, and 12 in the cared for experimental groups, therefore hatching success was not analysed further.

3. Results

Development started in 60 out of 78 eggs, and the probability of embryonic development was not statistically different between

deserted and cared for eggs (mean \pm SE of proportion of eggs starting to develop from each nest, deserted vs. cared for experimental groups: 0.57 ± 0.10 vs. 0.97 ± 0.03), after controlling for the effect of increased inactive period in deserted group (GLMM, care type: $\chi^2_1 = 2.32$; $P = 0.13$; inactive period: $\chi^2_1 = 14.37$; $P < 0.001$; Fig. 1a).

Embryo survival in the 60 eggs that started to develop was not different between deserted and cared for groups (Cox Mixed Model, care type: $\chi^2_1 = 0.02$; $P = 0.90$; Fig. 1b).

4. Discussion

Our results provide evidence that the viability of biparentally deserted penduline tit eggs are not different from those of cared for ones. These findings, therefore, do not support the offspring viability hypothesis as an explanation for the high frequency of biparentally deserted nests. Based on our earlier findings addressing sexual conflict and uncertain/low parentage hypotheses (van Dijk et al., 2010b; Szentirmai et al., 2007), we conclude that the most congruent explanation remains that biparental desertion is a costly by-product of intense sexual conflict over care between penduline tit parents.

If biparental desertion is costly for both parents in terms of wasted investment that could be otherwise spent on a different breeding attempt that produces young, we expect strong selection against this outcome. Why then, do we see high frequencies of biparental desertion across distant populations of Eurasian penduline tits with highly variable environmental conditions (van Dijk et al., 2010a)? The most plausible explanation is that over the lifetime of an individual, the benefits of offspring desertions outweigh their costs. Saving time and energy resources by refraining from care and seeking for additional mating opportunities instead are higher than what is lost at wasted breeding attempts due to biparental desertion, because the mate at some of the deserted nests will stay and care (Szentirmai et al., 2007; van Dijk et al., 2012). Our study further emphasizes the strength of sexual conflict over care, as desertion is a profitable strategy for both sexes, in spite of the substantial costs associated with biparental desertion. Furthermore, there seems to be no morphological or behavioral cues by which males and females can assess the desertion intention of their prospective mate at the time of pair formation (van Dijk et al.,

2007a) and/or parental decisions are not fixed and pair members 'decide' no sooner than during egg-laying.

Our study, admittedly, has limitations resulting mainly from constraints of fieldwork in the wetlands of the Danube delta. First, we kept constant conditions in the incubator for experimental considerations instead of changing parameters in the end of embryonic development to maximize hatching success (see Section 2.3. of methods). Admittedly, an experimental hatching success that is closer to what has been found in nature would have made it possible to compare the proportion of young produced from the two groups. We argue, nevertheless, that sub-optimal conditions likely facilitated the detection of any possible quality differences of offspring. Second, our analyses were restricted to a few proxies of viability and offspring survival, and it is possible that various aspects of offspring quality remained hidden. Our study investigates the possible link between innate offspring quality and parental decisions. We, therefore, did not follow the post-natal growth of experimental chicks cared for by real or foster parents, because parental care may compensate to an unknown degree for any possible differences in innate offspring quality. We nevertheless acknowledge that a comprehensive test of our hypothesis would focus on lifetime reproductive success of chicks fledged from the two experimental groups in the incubator. Third, there was a trend for more eggs to start developing in the cared for than in the deserted experimental group, mainly due to between-group differences in inactive period. Nevertheless, we acknowledge that a conclusive analysis would take a larger sample size so that a weaker group effect can be detected.

Although of the two components of reproductive value of current offspring, offspring quality was sparsely in focus, numerous empirical studies investigated how change in brood size predicts care decisions. In support of theory (Carlisle, 1982; Eadie and Lyon, 1998), decreased clutch or brood size (i.e., previous brood mortality) has been reported to predict offspring desertion in various species (e.g., Zwickel and Carveth, 1978; Poysa et al., 1997; Johnston, 2011; Armstrong and Robertson, 1988; Jennions and Polakow, 2001; Ackerman and Eadie, 2003). Nevertheless, we argue that the scope of sexual conflict with regards to offspring desertion may be under-estimated: studies of offspring desertion should take into account that sexual conflict may interact with various factors to facilitate desertion. For instance, sexual conflict may lower the threshold for tolerance of human disturbance, low food resources, reduction in brood size (e.g., in the above examples) or of any other environmental factors leading to a decreased value of the current brood. This view is supported by a recent study in house sparrows (*Passer domesticus*), in which experimental brood reduction had a stronger effect on desertion early in the breeding season than late, possibly reflecting a diminishing resource of mate availability to re-nest (Johnston, 2011).

Taken together, the results reported here confirm our previous results (van Dijk et al., 2012; Szentirmai et al., 2007), and further emphasize the intensity of sexual conflict over care by identifying it as the main driver of offspring desertion in Eurasian penduline tits. Biparental offspring desertion seems to be a mutually costly by-product of sexual conflict over care, as these eggs could potentially produce viable young. The fitness costs of desertion strategy are (over) balanced by its benefits when the mate cares; nevertheless, the high frequency of biparental desertion implies that both the costs and the benefits associated with desertion strategy are large.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2015.04.014>.

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