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PARENTAL BEHAVIOR AND REPRODUCTIVE OUTPUT IN MALE-ONLY CARED AND FEMALE-ONLY CARED CLUTCHES IN THE EURASIAN PENDULINE TIT

(REMIZ PENDULINUS)

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ABSTRACT.—Diverse patterns of parental care, including uniparental care by either the male or the female, provide excellent opportunities to investigate how variation in social traits is maintained in wild populations. Coexistence of different parental strategies within the same population is expected when they exhibit similar cost–benefit ratios. We investigated one of the most diverse avian breeding systems and compared parental behavior and reproductive output between nests that are uniparentally cared for by male or female Eurasian Penduline Tits (*Remiz pendulinus*). In this small passerine bird, full care (incubation and brood care) is provided by the male only (7–18% of nests) or the female only (48–65% of nests). Additionally, a third of all nests are deserted by both parents as a result of intense sexual conflict over care. We show that parental effort is similar between male and female parents, and they achieve similar offspring survival after controlling for clutch-size differences. Females care for larger clutches than males (5.7 ± 0.1 [SE] and 3.5 ± 0.2 eggs, respectively), and they produce more nestlings (3.6 ± 0.2 and 2.4 ± 0.3 nestlings, respectively), although this difference is not significant at fledging of the chicks (3.1 ± 0.2 and 2.4 ± 0.3 young, respectively). Therefore, sex difference in care does not explain the bias toward female-only care in Eurasian Penduline Tits. We propose that the differential benefits of desertion and/or the differential costs of care for males and females facilitate the existence of both uniparental care types in the population. *Received 18 April 2012, accepted 2 July 2012.*

Key words: breeding system, Eurasian Penduline Tit, parental care, *Remiz pendulinus*, sex role, sexual conflict.

Comportamiento Parental y Rendimiento Reproductivo en Nidadas Cuidadas Sólo por Machos o Sólo por Hembras en *Remiz pendulinus*

RESUMEN.—Diversos patrones de cuidado parental, incluyendo el cuidado uniparental por alguno de los padres, proveen excelentes oportunidades para investigar cómo las variaciones en los rasgos sociales se mantienen en las poblaciones silvestres. Se espera que diferentes estrategias parentales coexistan en de la misma población cuando ellas exhiben un balance similar entre costos y beneficios. Investigamos uno de los sistemas reproductivos más diversos en las aves, y comparamos el comportamiento parental y el rendimiento reproductivo entre nidos con cuidado uniparental de machos o de hembras de *Remiz pendulinus*. En esta pequeña ave paserina, todo el cuidado (incubación y empollamiento) es provisto sólo por los machos (7-18% de los nidos) o sólo por las hembras (48-65% de los nidos). Además, un tercio de todos los nidos es abandonado por ambos padres como resultado de un conflicto sexual intenso por el cuidado de las crías. Demostramos que el esfuerzo parental es similar entre machos y hembras, y que los sexos alcanzan una supervivencia de las crías similar después de controlar por diferencias en el tamaño de la nidada. Las hembras se hacen cargo de nidadas más grandes que los machos (5.7 ± 0.1 [EE] y 3.5 ± 0.2 huevos, respectivamente), y producen más pichones (3.6 ± 0.2 y 2.4 ± 0.3 pichones, respectivamente), aunque esta diferencia no es significativa en el momento del emplumamiento (3.1 ± 0.2 y 2.4 ± 0.3 crías, respectivamente). De este modo, las diferencias entre sexos en el cuidado parental no explican el sesgo hacia el cuidado sólo por parte de las hembras en *R. pendulinus*. Proponemos que los beneficios diferenciales del abandono del nido y/o de los costos diferenciales del cuidado por parte de hembras y machos facilitan la existencia de los dos tipos de cuidado parental en la población.

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Parental care is a highly diverse trait among animals, and examples of uniparental, biparental, and no parental care exist (Clutton-Brock 1991, Reynolds et al. 2002). In most bird species, both the male and the female share rearing of the young (Ligon 1999, Cockburn 2006), although uniparental care by the male or the female also occurs in a variety of taxa (Ligon 1999, Bennett and Owens 2002, Cockburn 2006). The origin and maintenance of this variation are hotly debated (Burley and Johnson 2002, Owens 2002, Kokko and Jennions 2008, McGraw et al. 2010); however, one consensus among researchers is that estimating the costs and benefits of care for the male and the female is essential to reveal how selection shapes care patterns. Species that exhibit mixed strategies (i.e., both male-only care and female-only care coexist in the same population) provide excellent opportunities to test the evolutionary theories of parental care (Székely et al. 1996, Webb et al. 1999, McNamara et al. 2002).

Estimating the costs and benefits of male-only and female-only care in natural populations is important to assess whether selection is maintaining the existing variation or eliminating one of these strategies (Clutton-Brock 1991). This is rarely done, and previous studies provided ambiguous results. Male-only and female-only care in the Galilee St. Peter's Fish (*Sarotherodon galilaeus*) and the burying beetle (*Nicrophorus vespilloides*) yielded similar number of offspring (Balshine-Earn 1997, Walling et al. 2008), whereas male and female Rock Sparrows (*Petronia petronia*) differed in their feeding effort and, consequently, more offspring were produced by females (Griggio and Pilastro 2007). Although studies often compared offspring growth and survival by experimentally removing the male or the female parent (reviewed by Clutton-Brock 1991, Liker 1995, Sanz et al. 2000, Harrison et al. 2009), the results of experimental studies are not directly comparable to observational studies, because in the former the parents were "forced" to provide care and, thus, their response may not reflect how selection acts in nature.

Here, we investigate one of the most suitable avian species for the analysis of the evolution of parental care: the Eurasian Penduline Tit (*Remiz pendulinus*). This small passerine (body mass ~9 g) has an unusually diverse breeding system that includes uniparental care of the clutch and young by the male or the female (Persson and Öhrström 1989). All populations that have been studied exhibit variable care patterns that are consistent across populations (Pogány et al. 2008, van Dijk et al. 2010a). Previous studies argued that the interests of male and female Penduline Tits are different and that this conflict of interest (sexual conflict over parental care; Arnqvist and Rowe 2005, van Dijk and Székely 2008) leads to mixed breeding systems in Penduline Tit populations (Persson and Öhrström 1989, Hoi et al. 1994, Valera et al. 1997, Szentirmai et al. 2007, van Dijk et al. 2012).

Seminal studies by Persson and Öhrström (1989) and Valera et al. (1997) were insightful, although they provided limited information on parental behavior and reproductive output at male-only cared and female-only cared nests. Quantifying parental behavior is important for assessing whether the costs and benefits of care are different for the sexes. Here we compare incubation, offspring provisioning, offspring size, offspring survival, and nest productivity between Penduline Tit nests with male-only or female-only care. On the basis of theoretical models (Webb et al. 1999, McNamara et al. 2000), we conjectured that male and female parents incubate the eggs and provision the young at comparable rates, and, consequently, that offspring survival will not be different between nests with male-only or female-only care. Thus, despite differences in the frequency of male-only and female-only care within a population, selection should favor the maintenance of this unusual parental care system.

Methods

Study species.—Penduline Tits arrive in early April at our field site in Fehértó, southern Hungary (46°19′N, 20°5′E), which is an extensive system of 16 fish-pond units separated by dikes (1,321 ha in total). Males immediately start building their pouch-shaped, domed nests mostly on willow (*Salix* spp.) and poplar (*Populus* spp.) trees along the dikes. During nest building, males sing to attract females, and the nest is often finished by the pair working together. If a male fails to attract a female, he will abandon his (often incomplete) nest and may start building a new nest in the vicinity (Mészáros et al. 2006). During egg laying (most frequently when the clutch has 3 or 4 eggs; van Dijk et al. 2007a), one or both parents desert the offspring, nest, and mate (Persson and Öhrström 1989). The species is highly polygamous; the deserting males and females search for a new mate, so that a single male or female may have up to six mates in a given breeding season (Persson and Öhrström 1989, Szentirmai et al. 2007). Previous studies in the Penduline Tit showed that desertion is beneficial for both males and females, even at the costs of the unusually high frequency of biparental desertion (about 28–40% of nests), in that the mate will stay and care for the eggs and chicks at some of the deserted nests (Szentirmai et al. 2007, Pogány et al. 2008, van Dijk et al. 2012). If the female stays to care, she continues laying eggs and, thus, female-only cared clutches are usually larger than male-only cared clutches (see below; Persson and Öhrström 1989). The incubation period lasts for ~14 days, and the young are provisioned for ~21 days before they fledge. The breeding season usually ends in August, after which Penduline Tits usually leave our study area and probably disperse and/or migrate southward.

Field work.—We studied Penduline Tits between April and August in 2002–2007. We searched for new nests and checked existing ones approximately every other day throughout the breeding season. Male and female Penduline Tits were captured using mist nets combined with song playback near the nest, or a specially designed nest trap (see van Dijk et al. 2007b). Birds were banded with a numbered aluminum band of the Hungarian Ornithological Institute and a unique combination of three color-bands (A.C. Hughes, Middlesex, United Kingdom). Adults have sexually dimorphic plumage that makes the sexes easy to distinguish in the field: males have large black masks and are more colorful overall than females (Pogány and Székely 2007, Kingma et al. 2008). To avoid nest abandonment, we mist netted only at nests that were in advanced stages of building (at least in stage C; see our field protocol [van Dijk et al. 2007b]) or were already incubated for ≥8 days. In both cases, a capture effort lasted for <30 min; if capture failed, we tried again on the next day. Penduline Tits are tame and tolerate humans near their nest. Nevertheless, to minimize disturbance, the nests were observed using binoculars from ≥15 m every other day to follow breeding status on the basis of parental behavior. For a more detailed description of field-work methods, nest checks, and capture and observation of Penduline Tits, see our field protocol (van Dijk et al. 2007b; also see Szentirmai et al. 2005a, van Dijk et al. 2007a).

We recorded incubation and provisioning at male-only cared (MC) and female-only cared (FC) clutches (or broods) between 2005 and 2007. Incubation was recorded at 28 nests (9 MC and 19 FC) for ~3 h (mean ± SE = 2.8 ± 0.1 h) between the 7th and 10th

days of incubation. If the incubating parent was captured during this period, we waited at least 1 day before recording his (or her) behavior. Recording started at a randomly selected time between 0600 and 1600 hours (Central European Standard Time, GMT + 1 h). We used a Sony (DCR-TR7000) Hi8 and a Panasonic (NV-DS28EG mini DV) digital recorder mounted on a tripod 15 m from the nest, so that the incubating parent was not disturbed.

Using video recordings or direct observations, we sampled offspring provisioning at 30 nests (10 MC and 20 FC) for ~2.5 h (2.6 ± 0.1 h) on the 10th day after hatching, starting randomly between 0600 and 1600 hours. In both 2005 and 2006, feeding visits at 24 nests (7 MC and 17 FC) were observed from a blind 15 m from the nests. In 2007, feeding visits were determined from video recordings at 6 nests (3 MC and 3 FC) using the same devices we used to record incubation behavior. At 11 nests, we collected both incubation and provisioning behaviors, whereas at 18 nests and 19 nests either incubation or provisioning was recorded, respectively.

To investigate the reproductive output that each care strategy produced (hereafter "offspring survival" and "nest productivity"), nests were monitored in 2002–2007 in four subsequent reproductive stages; nest productivity, corresponding to these stages, is (1) clutch size (counted between days 7 and 10 of incubation; see below), (2) number of hatchlings, (3) brood size at day 10, and (4) number of fledglings. Penduline Tit nests are usually difficult to reach; to minimize disturbance, we determined clutch size and brood size on the day when incubation behavior or offspring provisioning, respectively, was recorded at a given nest. Brood size at day 10 is a good estimate of the number of fledglings because these two variables are highly correlated in our population (Kingma et al. 2008).

Offspring survival was calculated as the proportion of eggs that produced 10-day-old nestlings at a given nest. Because recording the number of hatchlings and fledglings accurately can take considerable time and effort, these measures of nest productivity were collected at only a subset of nests in 2002–2004. Therefore, offspring survival analysis has larger sample size (142 nests: 33 MC and 109 FC) than nest productivity analysis (47 nests: 7 MC and 40 FC). Our recent genetic analysis based on microsatellite markers found similar rates of extrapair young in MC and FC nests, which

suggests that the number of offspring is a reasonable proxy of reproductive output for a given care type (van Dijk et al. 2010b).

To estimate nestling size, we measured both body mass and tarsus length of nestlings 11.0 ± 0.3 days after hatching in 87 broods (17 MC and 70 FC) between 2002 and 2004.

Sample sizes vary among analyses because we used the maximum information for each analysis (Table 1). Sample sizes for MC tend to be smaller, because fewer nests are cared for by males than by females. Most parents were individually banded (Table 1), and each banded parent contributed a single datum for a given analysis. Because return rates are low in Penduline Tits (<10% of adult return between years for each sex; van Dijk et al. 2008) and our study population is relatively large, it is unlikely that a nonbanded individual provided more than a single record to our data sets. We consider nest (or brood) as the unit of analysis.

Data processing and statistical analyses.—From the incubation video footage, we noted the times in each incubation bout when the parent (1) arrived at the nest and (2) left it. We defined incubation time as the proportion of time spent inside the nest. The parents may not make full contact with the eggs during the entire time inside the nest; however, given the small size of the pouch-shaped nest chamber, the parents' body heat is likely to influence internal nest (and thus egg) temperature (Szentirmai et al. 2005b). Therefore, we use the time spent inside the nest as a proxy for the time spent incubating.

We calculated offspring provisioning rates as nest visits per hour at each nest from feeding observations and video recordings. Nest visits without food delivery were rare (maximum = 2 of 68 ± 5 visits during 2.5-h observation periods; $n = 5$ nests), so we used the total number of nest visits to calculate offspring provisioning rate. We controlled for the possible confounding effects of ambient temperature and wind speed on parental behavior (Conway and Martin 2000) using data from the closest meteorological station of the Hungarian Meteorological Service (Sándorfalva station, 46°22′N, 20°06′E, approximately 5 km from our field site).

We used general linear models (GLMs) to examine the effects of the care-giving sex (male or female), ambient temperature, and wind speed on incubation time (arcsine transformed) and offspring

TABLE 1. Numbers of Eurasian Penduline Tit nests used in statistical analyses. Sample sizes are given separately for male-only cared (MC) and female-only cared (FC) nests in each year. Numbers of banded and unbanded individuals are also indicated.

		Incubation behavior	Provisioning rate	Clutch size	Offspring survival	Nest productivity	Nestling size
2002	MC; FC			13; 46	9; 29	3; 12	8; 24
	Total			59	38	15	32
2003	MC; FC			11; 32	6; 19	3; 15	6; 18
	Total			43	25	18	24
2004	MC; FC			6; 37	5; 34	1; 13	3; 28
	Total			43	39	14	31
2005	MC; FC	1; 9	3; 8	4; 12	1; 10		
	Total	10	11	16	11		
2006	MC; FC	4; 8	4; 9	8; 16	7; 14		
	Total	12	13	24	21		
2007	MC; FC	4; 2	3; 3	6; 6	5; 3		
	Total	6	6	12	8		
MC; FC		9; 19	10; 20	48; 149	33; 109	7; 40	17; 70
Total		28	30	197	142	47	87
Banded parent		21	22	149	104	36	70
Unbanded parent		7	8	48	38	11	17

provisioning rate (response variables). Because clutch and brood size differed between MC and FC nests, we controlled for clutch or brood size in all models. In initial models, the effects of year, time of day, and egg-laying dates were also included, because these may influence behavior via temperature and/or hormonal changes. Egg-laying dates were calculated as the number of days from 1 April until the date when the first egg of the clutch was laid.

Independent variables in models of offspring survival (dependent variable) included care-giving sex, clutch size, egg-laying date, and year. Offspring survival was analyzed in generalized linear models (GdLMs) with binomial error, in which brood size and clutch size were the nominator and denominator, respectively, of binomial distribution.

Nest productivity was analyzed in general linear mixed models (GLMMs). The initial model included number of offspring as a response variable, the four reproductive stages (see above), care-giving sex, and year as fixed factors; egg-laying date as a covariate; and nest ID as a random factor.

The mean body mass and tarsus length of nestlings were calculated for each brood, and we used both as dependent variables, separately, to investigate the effects of care-giving sex on offspring size using GLMs. Initial models of offspring size (dependent variable) included the care-giving sex, offspring age (in days), year, egg-laying date, and the number of hatchlings.

Assumptions of statistical tests were considered prior to the analyses. Statistical analyses were carried out in R, version 2.12.1 (R Development Core Team 2011). Model selection was done in a stepwise manner (direction of selection set to both forward and backward) based on Akaike's information criterion until the final models were reached. We tested for two-way interactions between care-giving sex and the remaining explanatory variables in all the above initial models (and retested in final models), because these would indicate differential effects of care-giving sex in regard to specific explanatory variables. We provide statistics for excluded variables before their exclusion from the model. Mean ± SE and two-tailed probabilities are given, and we rejected the null hypotheses at $P < 0.05$.

Results

Care patterns and clutch size.—Between 2002 and 2007, females cared for 47.4% of clutches, males cared for 13.5% of clutches, and 39.1% of clutches were deserted by both parents ($n = 534$ clutches). No biparental care of eggs or young occurred. Female-only care was more common than male-only care (binomial test using 325 uniparental clutches and 0.5 expectation, $P < 0.001$), which is consistent with the results of other studies of Penduline Tits (Persson and Öhrström 1989, van Dijk et al. 2010a).

Females cared for larger clutches (5.7 ± 0.1 eggs, $n = 149$ clutches) than males (3.5 ± 0.2 eggs, $n = 48$ clutches; $t = 10.12$, df = 195, $P < 0.001$). Clutch size declined over the breeding season in most years (Fig. 1; see also Persson and Öhrström 1989, Hoi et al. 1994), and MC clutches were initiated later than FC clutches (Persson and Öhrström 1989, Szentirmai et al. 2005a, Pogány et al. 2008). However, the different egg-laying dates did not account for larger clutch size of FC clutches: when both egg-laying date (GLM, $F = 19.75$, df = 1 and 189, $P < 0.001$, $n = 197$ nests) and year ($F = 2.87$, df = 1 and 189, $P = 0.016$) were included in the models, FC clutches remained significantly larger ($F = 117.20$, df = 1,189, $P < 0.001$). The interaction term between care-giving sex and egg-laying date was not significant ($F = 0.34$, df =1 and 188, $P = 0.560$;
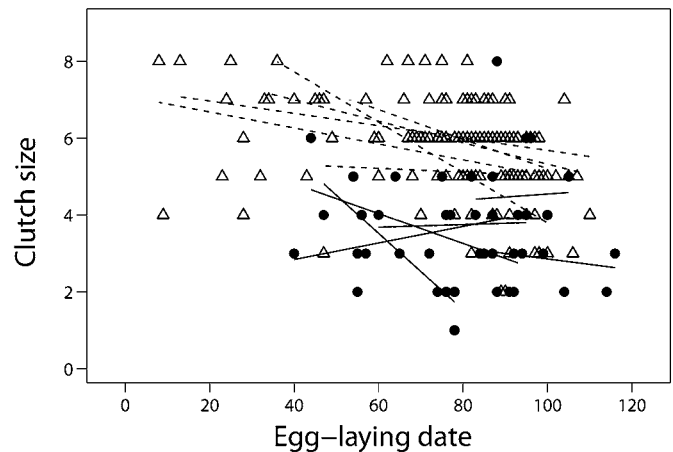

Fig. 1. Clutch size in nests with male-only cared (filled circles, $n = 48$) or female-only cared (open triangles, $n = 149$) in relation to egg-laying date in Eurasian Penduline Tits. Egg-laying date is the number of days between 1 April and the date when the first egg of the clutch was laid in each year. Regression lines are fitted for males (solid lines) and females (dashed lines) and for each year (2002–2007) separately.

Fig. 1), which suggests that the seasonal decline in clutch size was not different between MC and FC clutches; therefore, this interaction was not included in the final model ($R^2 = 0.45$, $P < 0.001$).

Parental effort.—Both males and females decreased incubation time as ambient temperature increased (GLM, $F = 31.47$, df = 1 and 26, $P < 0.001$, $n = 28$ clutches; Fig. 2), but despite this, and the difference in the size of the clutches tended by the sexes,
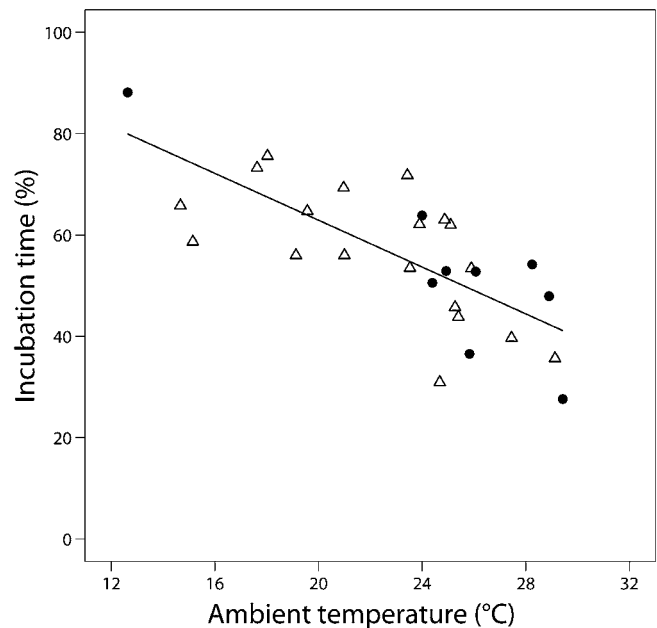

Fig. 2. Incubation time of Eurasian Penduline Tits in relation to ambient temperature. Incubation time is the percentage of time that the parent (male or female) spent inside the nest. Filled circles indicate male-only cared nests ($n = 9$), and open triangles indicate female-only cared nests ($n = 19$).

male and female parents did not differ significantly in the time they spent incubating ($F = 0.38$, df = 1 and 25, $P = 0.544$). The sexes reacted to weather changes comparably (care-giving sex * ambient temperature interaction: $F = 1.66$, df = 1 and 24, $P = 0.210$). Incubation time was also independent of clutch size ($F = 0.42$, df = 1 and 25, $P = 0.526$), wind speed ($F = 0.04$, df = 1 and 25, $P = 0.846$), egg-laying date ($F = 0.24$, df = 1 and 25, $P = 0.628$), time of day ($F = 1.97$, df = 1 and 25, $P = 0.173$), and year ($F = 1.00$, df = 2 and 25, $P = 0.382$), so that these were excluded from the final GLM ($R^2 = 0.55$, $P < 0.001$).

Provisioning rate (nest visits per hour) varied among years (GLM, $F = 14.88$, df = 2 and 26, $P < 0.001$, $n = 30$ broods) and increased with brood size ($F = 36.85$, df = 1 and 26, $P < 0.001$; Fig. 3). After accounting for the latter variables, the provisioning rates did not differ between male and female parents ($F = 0.51$, df = 1 and 25, $P = 0.483$). Additionally, provisioning rates increased with brood size in both MC and FC nests (care-giving sex * brood size interaction: $F = 0.03$, df = 1 and 24, $P = 0.858$; Fig. 3). Provisioning rate was independent of ambient temperature ($F = 0.93$, df = 1 and 25, $P = 0.344$), wind speed ($F = 0.15$, df = 1 and 25, $P = 0.702$), egg-laying date ($F = 0.03$, df = 1 and 25, $P = 0.865$), and time of day ($F = 0.89$, df = 1 and 25, $P = 0.356$); therefore, these variables were not included in the final model ($R^2 = 0.72$, $P < 0.001$).

Offspring survival.—Offspring survival (proportion of eggs to produce 10-day-old nestlings) did not differ between MC and FC nests but declined with increasing clutch size and with egg-laying date (Table 2 and Fig. 4). Offspring survival declined more steeply in relation to clutch size in MC nests than in FC nests (as shown by a significant care-giving sex * clutch size interaction; Table 2). The latter interaction was driven by a single influential nest (an exceptionally large MC clutch of 8 eggs; Fig. 4), because the interaction term was no longer significant when this single influential
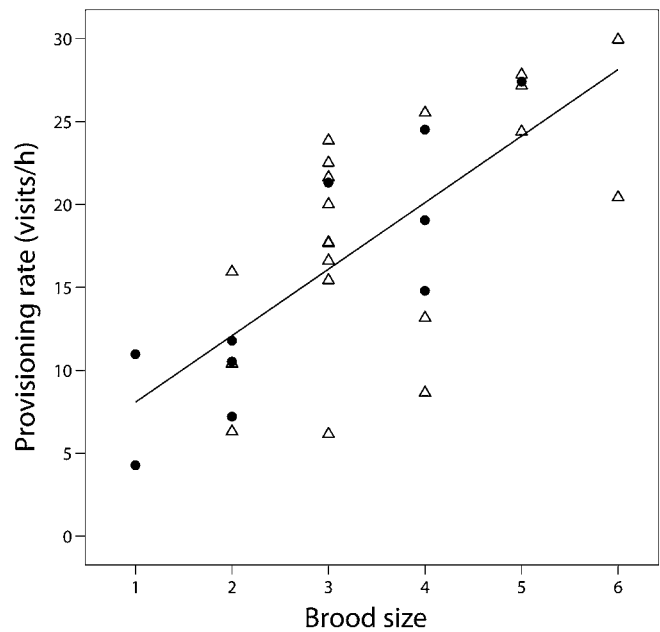

FIG. 3. Offspring provisioning rates at Eurasian Penduline Tit nests in relation to brood size. Filled circles indicate male-only cared nests ($n = 10$), and open triangles indicate female-only cared nests ($n = 20$).

data point was excluded (restricted analysis including nests with 2–6 eggs for both sexes, GdLM 2; Table 2). Offspring survival also decreased with egg-laying date, comparably in MC and FC nests (Table 2).

Nest productivity and nestling size.—Female-only cared clutches tended to produce more offspring in each reproductive

TABLE 2. Offspring survival (proportion of eggs that produced 10-day-old nestlings) in Eurasian Penduline Tit nests (2002–2007). Two generalized linear models (GdLM; with binomial error) of offspring survival are given; GdLM 1 included all 142 nests for which we had data (33 male-only cared [MC] and 109 female-only cared [FC] nests), whereas GdLM 2 was restricted to the 105 nests that contained 2 to 6 eggs (see text; 32 MC and 73 FC nests).

	Parameter estimate ± SE	χ^2	df	P
GdLM 1 offspring survival				
Explanatory variables in final model				
Clutch size	−0.46 ± 0.14	5.97	1	0.015
Egg-laying date	−0.01 ± 0.00	7.35	1	0.007
Care-giving sex	−2.25 ± 0.82	1.46	1	0.227
Care-giving sex * clutch size	0.41 ± 0.16	6.57	1	0.010
Excluded variables				
Year	(−0.15 to 0.52) ± (0.21–0.39)[a]	9.73	5	0.083
GdLM 2 offspring survival				
Explanatory variables in final model				
Clutch size	−0.31 ± 0.10	10.02	1	0.002
Egg-laying date	−0.01 ± 0.01	5.92	1	0.015
Excluded variables				
Care-giving sex	−0.32 ± 0.29	1.19	1	0.275
Care-giving sex * clutch size	0.45 ± 0.24	3.47	1	0.063
Year	(0.08–0.63) ± (0.30–0.48)[a]	5.82	5	0.324

[a]Parameter estimates and SE for categorical variables with more than two levels (year) are given by range over contrasts.
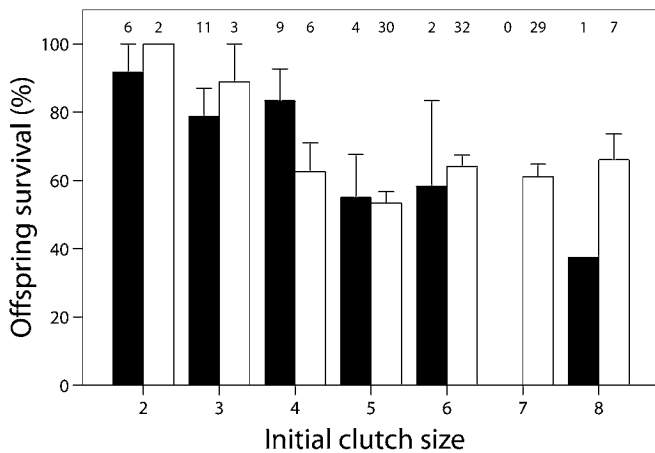
Fig. 4. Offspring survival in Eurasian Penduline Tits in relation to clutch size. Offspring survival is the percentage of eggs that produced 10-day-old nestlings. Filled bars indicate male-only cared nests (*n* = 33), and open bars indicate female-only cared nests (*n* = 109). Number of clutches is given above each bar; error bars show +1 SE.

stage (i.e., eggs, hatchlings, 10-day-old nestlings, and fledglings) than MC nests (GLMM, *F* = 19.75, df = 1 and 42, *P* < 0.001, *n* = 47 nests; Table 3 and Fig. 5). The difference in nest productivity between MC and FC nests decreased from clutch size to fledglings as indicated by a significant care-giving sex * reproductive stage interaction (*F* = 6.65, df = 3 and 135, *P* < 0.001; Table 3). Therefore, FC nests that had twice as many median eggs (Wilcoxon rank sum test, *W* = 272.5, *Z* = 4.09, n_{FC} = 40, n_{MC} = 7, *P* < 0.001, effect size: *r* = 0.60) yielded the same median number of fledglings as MC nests (*W* = 174.0, *Z* = 1.04, n_{FC} = 40, n_{MC} = 7, *P* = 0.304, effect size: *r* = 0.15; Fig. 5).

There was no difference in nestling size (mean body mass or mean tarsus length) between MC and FC nests (GLM, body mass: *F* = 0.63, df = 1 and 82, *P* = 0.428, *n* = 87 nests; tarsus length: *F* < 0.01, df = 1 and 82, *P* = 0.991; Table 4). Nestling mass decreased with egg-laying date and with the number of hatchlings (Table 4), whereas both nestling mass and tarsus length increased with nestling age (Table 4).

Discussion

Our comparison of male-only and female-only parental behavior and reproductive output provided two key results. First, we found no difference between male and female parental behavior. Incubation efforts of male and female Penduline Tits were comparable, despite the approximately twofold difference in clutch size. This suggests that clutch size had no influence on incubation behavior, although a laboratory experiment found that the cooling rate of a clutch of Penduline Tit eggs was influenced by clutch size (Szentirmai et al. 2005b). Field observations in various bird species also reported that clutch size influenced incubation effort (Haftorn and Reinertsen 1985, Dobbs et al. 2006). A possible explanation for this discrepancy is that Penduline Tits have well-insulated nests compared with many tree-hole (or nest-box) nesting passerines investigated by the aforementioned studies (Hoi et al. 1994, Szentirmai et al. 2005b). Furthermore, per offspring provisioning rates (i.e., after controlling for effects of brood size) were also comparable between the sexes. We note, however, that the absolute number of female feeding visits was higher because females fed larger broods, and this suggests that the cost of rearing the full brood is higher for the female than for the male.

Second, we showed that offspring survival is different in FC and MC nests, although this difference is driven by the initial clutch-size differences, rather than sex differences per se. In addition, neither nestling size nor the proportion of eggs to produce 10-day-old young differed between MC and FC nests. This is in line with parental behavior (see above) and does not exclude the possibility that uniparental care by males and females could produce similar numbers of offspring. We note, however, that our analysis of offspring survival was limited by natural clutch-size differences, so this prevented us from comparing offspring survival in large (7–8 eggs) MC and FC clutches. To address the latter question, one needs to simultaneously manipulate the deserting parent and clutch size. We did not carry out experimental manipulations, for two reasons. (1) We were interested in costs and benefits of natural behavior, and by experimentally manipulating clutch size we might have inflated the costs, the benefits, or both for males and females. (2) In a pilot study in 2010, we removed one parent randomly from six nests where males were paired on the second day of egg laying, and

Table 3. Nest productivity (number of offspring per nest) in Eurasian Penduline Tits (2002–2007). General linear mixed models (GLMM) of nest productivity included 47 nests (7 male-only cared and 40 female-only cared nests). Nest productivity (response variable) was recorded in four subsequent reproductive stages and corresponds to number of eggs, number of hatchlings, number of 10-day-old nestlings, and number of fledglings. Nest ID was included in the models as a random factor.

GLMM nest productivity	Parameter estimate ± SE	*F*	df	*P*
Explanatory variables in final model				
Reproductive stage	(–0.43 to –0.86) ± 0.48[a]	85.40	3	<0.001
Care-giving sex	2.44 ± 0.48	19.75	1	<0.001
Egg-laying date	–0.02 ± 0.01	10.83	1	0.002
Year	(0.68–1.08) ± 0.34[a]	5.23	2	0.009
Care-giving sex * reproductive stage	(–2.22 to –1.20) ± 0.52[a]	6.65	3	<0.001

[a]Parameter estimates and SE for categorical variables with more than two levels (reproductive stage, year, care-giving sex * reproductive stage) are given by range over contrasts.
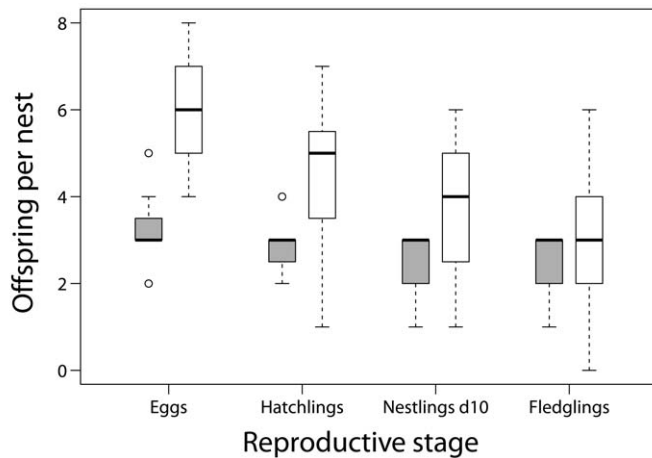
FIG. 5. Nest productivity in male-only cared and female-only cared Eurasian Penduline Tit nests from Hungary as offspring development advances. Box plots indicate the same nests in four subsequent reproductive stages (filled boxes: $n = 7$ male-only cared nests; open boxes: $n = 40$ female-only cared nests). "Eggs" represent clutch size, and "Nestlings d10" indicates the number of 10-day-old nestlings. Box plots show the median and 25th and 75th percentiles, whiskers indicate data points within 1.5 interquartile range from the first and third quartiles, and open circles represent outliers that do not fall within this range.

found that all six mates uniformly deserted the clutch (Á. Pogány et al. unpubl. data)—a behavioral response that we interpreted as the effect of disturbance.

Although the nests of female parents contained more eggs and nestlings than those of male parents, by fledging, this initial almost twofold difference has diminished and was no longer statistically significant. The diminishing difference with advancing reproductive stages may indicate that the increased demand of feeding more young has put a heavier burden on females than on males. This pattern, although indirect, suggests that the increased cost of care for larger clutches is not fully balanced by the increased benefit of more offspring produced by FC nests.

Our results are similar to those of previous studies in fishes and insects (Balshine-Earn 1997, Katvala and Kaitala 2001, Berglund and Rosenqvist 2003, Walling et al. 2008; but see Griggio and Pilastro 2007), in that none of these studies found different parental effort or offspring fitness between MC and FC broods. These studies together suggest that the two parental strategies (male-only vs. female-only care) may produce similar payoffs; indeed, this may contribute to the coexistence of the two strategies in the population. To ascertain the latter proposition, one would need to quantify postfledging survival and recruitment to a breeding population, although these are challenging given the low local recruitment rate in Eurasian Penduline Tits (van Dijk et al. 2008).

Why do female Penduline Tits provide uniparental care more frequently than males, given that productivity does not differ? First, with larger sample sizes, one might find a statistical difference in the number of fledglings of FC versus MC nests; however, this is unlikely given the small effect size in our analysis. Second, although our study focused on the benefits (and costs) of male-only and female-only care, for a comprehensive understanding of a variable breeding system it is also important to focus on the costs and benefits of offspring desertion (Székely et al. 1996, Gross 2005). Although Penduline Tits of either sex may increase their reproductive success by desertion (Szentirmai et al. 2007), the relative costs and benefits of desertion may still be different for males and females, so that the net gain by desertion is higher for the male (Queller 1997). Experimental studies carried out in two other species with flexible breeding systems, the Kentish Plover (*Charadrius alexandrinus*) and the Galilee St. Peter's Fish, suggested that biased adult sex ratio favors desertion of the less numerous sex because of increased remating opportunity

TABLE 4. Nestling size in male-only cared (MC) and female-only cared (FC) nests in Eurasian Penduline Tits (2002–2007). Two general linear models (GLM) of nestling size are given ($n = 87$ nests in both models: 17 and 70 MC and FC nests, respectively); GLM 1 included mean body mass as response variable, whereas GLM 2 included mean tarsus length of approximately 11-day-old nestlings. Final models: GLM 1: $R^2 = 0.36$, $P < 0.001$; GLM 2: $R^2 = 0.46$, $P < 0.001$.

	Parameter estimate ± SE	F	df	P
GLM 1 offspring body mass				
Explanatory variables in the final model				
Offspring age	0.17 ± 0.04	23.17	1	<0.001
Egg-laying date	-0.02 ± 0.00	11.22	1	0.001
Number of hatchlings	-0.24 ± 0.07	13.15	1	<0.001
Excluded variables				
Care-giving sex	-0.20 ± 0.25	0.63	1	0.428
Year	$(-0.47$ to $-0.12) \pm 0.26$[a]	1.73	2	0.184
GLM 2 offspring tarsus length				
Explanatory variables in the final model				
Offspring age	0.13 ± 0.03	44.22	1	<0.001
Year	$(-0.79$ to $0.23) \pm 0.19$[a]	13.77	2	<0.001
Excluded variables				
Egg-laying date	0.00 ± 0.00	0.13	1	0.722
Number of hatchlings	-0.00 ± 0.06	<0.01	1	0.974
Care-giving sex	0.00 ± 0.19	<0.01	1	0.991

[a]Parameter estimates and SE for categorical variables with more than two levels (year) are given by range over contrasts.

(Balshine-Earn and Earn 1998, Székely et al. 1999). Adult sex ratios are biased in many bird species (Donald 2007), and the full implications of sex ratio bias have yet to be identified. Additionally, one could compare the Bateman gradients of the sexes—that is, estimate the rate of increasing (or decreasing) reproductive success in relation to the number of mates for males and females separately (Bateman 1948, Arnold and Duvall 1994, Jones et al. 2000).

In addition to the above explanations, males may provide less care because they are uncertain about paternity (Birkhead and Møller 1995, Queller 1997, Kempenaers et al. 1998, Westneat and Stewart 2003). We argue, however, that this explanation is not likely in Penduline Tits; although 23.5% of offspring in our population were sired by an extrapair male, the proportion of extrapair paternity was not different between MC and FC nests (van Dijk et al. 2010b).

The reasons why a caring female may continue laying more eggs after her mate has deserted need further investigation. One potential explanation is that in years with less demanding environmental constraints, most chicks fledge and, thus, the extra eggs are translated into higher reproductive success, whereas in poor years there is strong brood reduction that eliminates the benefit of additional eggs. Likewise, seasonal trends in care patterns require further investigation. Previous studies identified three non-mutually-exclusive possibilities for later initiation of male care than female care in the season: (1) change in remating opportunities with advance of the breeding season (Persson and Öhrström 1989); (2) change in circulating hormone levels (Pogány et al. 2008); and (3) male seasonal trend, coupled with individually consistent female behavior, forming an optimal pair of strategies (Pogány et al. 2008).

In sum, our results in one of the most variable avian breeding systems, that of the Eurasian Penduline Tit, show that male and female parents fledge similar numbers of young. At the population level, however, more offspring are raised by female parents than by male parents because female-only care occurs more frequently than male-only care. Our results suggest that the bias toward more frequent female-only care is likely not explained by sex differences in parental behavior. Future work will need to address life-time reproductive success of males and females by accounting for the number of mates that each sex obtains (i.e., focusing on the benefits and costs of desertion) as well as the potentially sex-specific effects of reproduction on survival. Additionally, studies focused on the long-term effects of care-giving sex on postfledging offspring survival are needed for a better understanding of why these two parenting strategies coexist and why female Penduline Tits care more frequently for the offspring than males.

ACKNOWLEDGMENTS

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