

Parental Care, Male Desertion, and Reproductive Success in the Spanish Sparrow, *Passer hispaniolensis*

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Paulo A. M. Marques (2004) Parental care, male desertion, and reproductive success in the Spanish Sparrow, *Passer hispaniolensis*. *Zoological Studies* 43(1): 123-131. Parental care in altricial birds is costly, and mate desertion can occur due to sexual conflict over the level of parental investment in the offspring. This cessation of parental care by 1 parent can affect the success of the current reproduction. In the Spanish Sparrow (*Passer hispaniolensis*), the nests can either have bi-parental or female-only care. Males desert early in the breeding cycle. This study quantifies parental feeding effort and brooding behavior in nests with bi-parental or female-only care, and describes the impact of desertion on reproductive success. The absence of differences between sexes in bi-parental care nests suggests that males generated feeding efforts similar to females, but females performed a greater number of brooding visits. Bi-parental care nests presented higher total feeding effort compared to uni-parental care nests, but the average feeding care received by each nestling did not significantly differ between the 2 types of nests, due to the higher number of nestlings present in the bi-parental nests. From these results, we expect, as was observed, that nestling conditions were similar between uni- and bi-parental nests. Only hatching success differed between uni- and bi-parental nests, while other breeding success parameters did not significantly differ between nest types. Single females invested significantly more per nestling than did coupled female, having to provide more in order to feed the same number of offspring. These results suggest that single females compensated for the absence of male parental care in order to maintain their short-term fitness. <http://www.sinica.edu.tw/zool/zoolstud/43.1/123.pdf>

Key words: Reproductive behavior, Facultative male desertion, Parental effort, Passeridae.

Four possible patterns of parental care might be favored by natural selection: no care, uni-parental care by a male, uni-parental care by a female, and bi-parental care (Trivers 1972, Clutton-Brock 1991, Rosenblatt and Snowdon 1996). Evolutionarily stable strategy models suggest that bi-parental care is stable when parents partially compensate for changes in care by the other parent (Chase 1980, Houston and Davies 1985). Depending on several factors, other patterns can be stable (Webb et al. 1999, McNamara et al. 2000). In birds, bi-parental care is the most common pattern (Lack 1968, Gowaty 1996) although uni-parental care by either the male or female exists (Clutton-Brock 1991, Gowaty 1996, Szekely and Cuthill 1999). In species where both parents care for the young, a conflict of interests may occur due to differences in the optimal level

of investment in the brood for each partner (Trivers 1972), which may be influenced by factors such as availability of food, operational sex ratio, a mate's strategy, need for care of the brood, brood condition, relative importance of parental care to offspring survival, and in the case of males, relatedness with the offspring (Trivers 1972, Beissinger 1986, Lazarus 1990, Yasukawa et al. 1990, Whittingham et al. 1993). In this context, mate desertion by 1 parent may occur when his individual cumulative investment is exceeded by the partner's. The deserted one loses more than the deserter if no offspring are raised, and therefore would be more strongly selected to stay and care for the brood to maximize their future reproductive success (Trivers 1972).

Mate desertion occurs in some bird species (e.g., Snail Kite, *Rostrhamus sociabilis*, Beissinger

and Snyder 1987; Great Reed Warbler, *Acrocephalus arundinaceus*, Ezaki 1988; Penduline Tit, *Remiz pendulinus*, Persson and Öhrström 1989; Cooper's Hawk, *Accipiter cooperii*, Kelly and Kennedy 1993; Kentish Plover, *Charadrius alexandrinus*, Székely and Lessells 1993; Magnificent Frigatebird, *Fregata magnificians*, Osorno 1999; and Curlew, *Numerius arquata*, Currie et al. 2001).

As a result of the reduction of parental care by 1 parent, an adaptive interpretation predicts that the fitness payoff of the current offspring would be reduced (Trivers 1972, Lazarus 1990). This should result from a lower nest survival probability, lower number of fledglings produced, or poorer offspring condition. In the case of social polygamic species like House Wrens, *Troglodytes aedon*; Pied Flycatchers, *Ficedula hypoleuca*; or European Starlings, *Sturnus vulgaris*, where polygynous males predominately assist at primary nests, secondary nests have lower reproductive success (e.g., fledging fewer offspring; Harvey et al. 1988, Pinxten and Eens 1990, Johnson and Kermott 1993, Cramp and Perrins 1994). Also in male removal experiments in passerine species with high male contribution to feeding nestlings, females presented a reduction in reproductive success (reviewed in Møller 2000). On the other hand, the few studies on the effect of mate desertion on fitness generally report very small reductions in reproductive success, e.g., Snail Kite (Beissinger 1987) and Great Reed Warbler (Ezaki 1988).

The response of 1 parent to a reduction in parental care by its partner should be constrained by the value of the current reproduction and the cost associated with the decision to compensate for the reduction in care (Sanz et al. 2000). The decision to compensate should affect the fitness of the caregiver through an increase of the cost of the current reproduction. The current reproductive effort can influence the future survival of adults (e.g., Bryant 1988) and their future reproductive success (e.g., Gustafsson and Sutherland 1988).

The Spanish Sparrow, *P. hispaniolensis*, is usually described as a bi-parental species where both parents feed the young (Metzmacher 1990). However, at least in 1 population, apparent male mate desertion has been observed (Marques 2003). Male mate desertion is facultative (i.e., males can either stay and care for the nestlings or abandon the nest) and varies greatly between years (from 5.9% to 37.9% of nests). Desertion usually occurs early in the breeding cycle, during incubation (Marques 2003).

This study focused on differences in parental provisioning between uni- and bi-parental care nests and analyzed the consequences of male mate desertion on short-term measures of fitness. The questions addressed included the following i) whether males and females present different provisioning efforts in bi-parental nests; ii) whether desertion affects the amount of parental care received by the nestlings; and iii) whether desertion has an effect on fitness. This issue was addressed through an evaluation of the impact of desertion on short-term measures of fitness and on the condition of nestlings. Finally we determined whether desertion by 1 parent affected the parental effort of the parent remaining with the offspring by comparing the provisioning effort of deserted and paired females.

MATERIALS AND METHODS

The study was carried out in 2000 and 2001 from early Mar. to mid June at Castro Verde in southern Portugal (37°41'N, 08°03'W). The region is a cereal steppe with cereal crops alternating with fallow ground. Small *Eucalyptus* plantations and olive groves abound in the area. Fallow ground usually consists of land used for grazing sheep and cows. The study area was regularly visited to monitor Spanish Sparrow nesting colonies. The Spanish Sparrow is a gregarious species with highly synchronized breeding (Alonso 1984, Marques et al. 2002). When the colonies are being formed, males choose the nest place and defend it from other males. Nest construction is performed mainly by the male, with the female completing the lining (Gavrilov 1963, Alonso 1982). The nest is roughly spherical, with the entrance hole in the side.

In total, 43 nests were studied in 4 colonies: 17 in 2000 and 26 in 2001 (in 1 nest no quantitative data were collected due to technical problems, but bi-parental care was confirmed). The breeding season of this species lasts approximately 3 mo in this region starting in the end of Mar. or beginning of Apr. The colonies were classified as "early season" if most of the breeding occurred in Apr. (2 colonies, 16 nests) and "mid-season" if it mainly occurred in May (2 colonies, 26 nests).

Parental visits were observed from a hide 15-20 m from the nest with the help of an 18-60x telescope. Each nest was observed for approximately 2 h (2.00 ± 0.02 h), avoiding the early morning and late afternoon periods where feeding rates are

lower (e.g., Rytkönen et al. 1996). Observations began after a waiting period (± 5 min) to allow adults to resume their normal feeding activities. At the time of the observation, the age of the oldest nestling ranged between 4 and 6 d (hatching day = day 1). Since birds were not individually marked, other individuals could have attended the nests.

Male mate desertion occurred in 9 of the 43 studied nests (20.93%, 6 in 2000 and 3 in 2001). Nests were considered deserted by males if no male visit was detected during the observation period (Marques 2003).

Nestling mass and tarsus length were measured after the observation period, and nestling body mass was linearly related to the length of the tarsus (mass = $-7.20 + 1.68$ tarsus, $n = 140$, $F = 951$, $r^2 = 0.87$, $p < 0.05$). The residual mass of each chick in the nest was used to determine the average nestling body condition, compensating for age and size differences.

Parents usually stopped briefly when arriving the nest, perching in a branch near the nest entrance hole, allowing us to record the delivered food load. Each food item delivered was scored as one of 5 load size classes, using bill size as a scale (1: no food visible but exhibiting feeding behavior; 2: 1 small item; 3: 2 small items or a large one; 4: 2 large items or several small ones; and 5: 3 or more large items); usually prey type could not be identified.

To describe parental care expenditure, we used the following parameters of brooding behavior and parental feeding: i) percentage of brooding time (brooding activities were assumed when parents stayed inside the nest for more than 2 min); and ii) mean duration of brooding visits and brooding visit rate (number of visits/h). These measurements were used both in an analysis of the total nest investment and to evaluate each sex's contribution to bi-parental care nests. The parameters for characterizing the feeding effort were: i) feeding rate (number of feeding visits/h); ii) feeding rate per nestling; iii) food delivery rate (total score of food load delivered/h); iv) food delivery rate per nestling; and v) average load size per visit.

All nests were monitored every 2-4 d to assess clutch size, number of hatchlings, number of nestlings at the age of 5 and 9 d old, and number of fledglings. A nestling was considered to have successfully fledged if it survived until the 11th day after hatching. Nests were considered successful if they produced at least 1 fledgling. Hatching success was calculated as the percent-

age of hatched eggs from all laid eggs. Breeding success was calculated as the percentage of young fledged from laid eggs considering all studied clutches.

We used the ratio between the female expenditure per nestling (feeding visit rate and food delivery rate) and the mean nest offspring condition (the residual mass was added to the average nestling body mass of the studied nests (11.7 g) to illustrate the actual weight of the nestlings and to avoid values near 0) as an index of female expenditure efficiency. Higher values characterized lower efficiency.

Percentages of brooding time (total per nest, females and males) were analyzed after arcsine square root transformation to attain homoscedasticity and normality. Logarithmic ($x+1$) transformations were made to heteroscedastic variables. Preferential one- and two-way ANOVAs for unbalanced design were used. When the assumptions of the ANOVAs were not met, non-parametric Mann-Whitney U tests were used.

Male and female behaviors in bi-parental nests were compared using the non-parametric Wilcoxon paired sample test due to heteroscedasticity of some parameters. In the multivariate analysis of the effect of nest parental care pattern and season in male and female brooding behavior, the mean duration of brooding visits was excluded to avoid diminution of the number of valid cases.

Statistical analysis was performed using Statistica software (StatSoft 1996). Results are presented as the mean \pm SE (standard error of the mean). The cut-off for significance was set at 0.05.

RESULTS

Males versus females in bi-parental care nests

We performed an analysis to evaluate the contribution of each sex to parental care in bi-parental care nests. When we examined the parameters used for studying brooding activities, we found that males and females presented different behaviors. Females spent more time brooding and performed more brooding visits, but with similar average durations (Table 1).

Female brooding behavior was similar in the 2 studied years. However, it varied significantly between early- and mid-season colonies (two-way ANOVA multivariate test, year Rao $R(2,28) = 0.93$, $p > 0.40$; season Rao $R(2,28) = 13.30$, $p < 0.0001$;

and year x season $R(2,28) = 0.68$, $p > 0.50$). All brooding parameters revealed a season effect (percentage of brooding time ANOVA $F(1,29) = 26.26$, $p < 0.0001$; brooding visit rate ANOVA $F(1,29) = 12.87$, $p < 0.01$, confirmed with post-hoc Tukey's test ($\alpha = 0.05$)). Similar results were obtained for duration of brooding visits (two-way ANOVA, year $F(1,25) = 0.81$, $p > 0.30$; season $F(1,25) = 15.99$, $p < 0.0005$; and year x season $R(1,25) = 0.44$, $p > 0.51$). All parameters decreased between early- and mid-season colonies (mean percentage of brooding time 24.14% and 16.40%; brooding visit rate 2.70 and 1.72 brood visits/h; duration of brooding visits 466s and 256s, respectively).

Male brooding behavior changed between years and seasons (two-way ANOVA multivariate test, year Rao $R(2,27) = 6.86$, $p < 0.004$; season Rao $R(2,27) = 4.02$, $p < 0.03$; and year x season Rao $R(2,27) = 3.02$, $p > 0.80$) with both factors presenting significant effects on the percentage of brooding time and brood visit rate. The duration of the brooding visits showed no significant effect of year or season (two-way ANOVA, year $F(1,14) = 0.04$, $p > 0.80$; season $F(1,14) = 1.20$, $p > 0.20$; and year x season Rao $R(1,14) = 2.40$, $p > 0.20$).

Males spent more time brooding and performed more brooding visits in early- than in mid-season colonies (early 16.11% and mid-season 5.94% and early 1.77 and mid-season 0.77, respectively), following the tendency of the decrease in female brooding time with season.

The analysis of male and female parental feeding behavior revealed no differences between sexes (Table 1). The male's share of the total parental feeding expenditure was approximately 50% for both the feeding visit rate ($49.07\% \pm 0.02\%$) and food delivery rate ($49.56\% \pm 0.02\%$), but greatly varied ranging from 23.07% to 78.95%

for the feeding visit rate and from 31.58% to 75.0% for the food delivery rate.

No year or season effect was detected in the nestling feeding parameters of females from bi-parental nests (two-way ANOVA multivariate test, year Rao $R(5,25) = 0.87$, $p > 0.50$; season Rao $R(5,25) = 1.67$, $p > 0.10$; and year x season $R(5,25) = 1.70$, $p > 0.10$). Univariate tests produced similar results for all parameters.

Overall male nestling feeding behavior was similar to that of females, and there were no effects of year or season (two-way ANOVA multivariate test, year Rao $R(5,25) = 1.79$, $p > 0.15$; season Rao $R(5,25) = 1.36$, $p > 0.20$; and year x season $R(5,25) = 2.54$, $p > 0.05$). However, univariate tests revealed an effect of season in the male food delivery rate per nestling (ANOVA $F(1,29) = 5.61$, $p < 0.05$, which was confirmed with post hoc Tukey's test ($\alpha = 0.05$)), with higher food delivery scores to each nestling in mid-season (early in the season 2.29 ± 0.21 ($n = 14$), and mid-season 2.99 ± 0.24 ($n = 19$)).

Uni-parental versus bi-parental care nests

A preliminary analysis revealed that all brooding parameters changed significantly with year (ANOVA multivariate test Rao $R(3,34) = 3.62$, $p < 0.03$). For feeding parameters, only the food delivery rate showed a significant year effect (ANOVA multivariate test Rao $R(5,36) = 2.39$, $p > 0.05$; food delivery rate ANOVA $F(1,36) = 4.7$, $p < 0.04$).

Due to the effect of year on the brooding parameters, only the nests from 2000 were used to study the effect of the pattern of parental care and season on parent brooding behavior. No effect of the 2 factors was detected on the brooding parameters, as parents presented similar brooding commitments between seasons and types of

Table 1. Comparison of male and female parental expenditures 5 d after nestling hatching in bi-parental nests

	Male		Female		Wilcoxon test		
	Mean \pm SE	N	Mean \pm SE	N	T	p	n
Brooding visit duration (s)	357 \pm 34	18	358 \pm 32	29	51	n.s.	17
Brooding visit rate	1.0 \pm 0.2	33	1.9 \pm 0.2	33	42	0.001	33
Percent of time brooding	10.3 \pm 2.6%	33	19.7 \pm 2.8%	33	81	0.005	33
Feeding visit rate	4.7 \pm 0.5	33	4.1 \pm 0.3	33	180	n.s.	33
Feeding visit rate/nestling	1.3 \pm 0.1	33	1.2 \pm 0.1	33	192	n.s.	33
Food delivery rate	9.6 \pm 0.8	33	8.9 \pm 0.5	33	222	n.s.	33
Food delivery rate/nestling	2.7 \pm 0.2	33	2.7 \pm 0.2	33	232	n.s.	33
Load size	2.2 \pm 0.1	33	2.2 \pm 0.1	33	270	n.s.	33

parental care to nestlings 5 d old (Table 2). The sample size of deserted nests in 2001 was insufficient to perform a between-year comparison.

Using data from both years, we found that only the parental care pattern had a significant effect on feeding parameters (Table 3). The analysis was performed without the food delivery rate due to the year effect, but the inclusion of the food delivery rate in the ANOVA produced similar results. Analysis of the effect of the parental care pattern on the different feeding parameters revealed that the total parental feeding expenditure, in number of feeding visits, was significantly different between the bi-parental and female-only care nests. Bi-parental nests received more feeding visits (Table 3). These differences disappeared when I compared the feeding effort per nestling, resulting in a similar effort per nestling in bi-parental and uni-parental care nests (Table 3). This observation may have been due to the difference in brood size between uni- and bi-parental nests (ANOVA $F(1,40) = 6.36$, $p < 0.016$). The average food load size delivered per visit to the nest was similar between the 2 types of nests (Table 3). The season effect was only significant in the food delivery rate per nestling, with mid-season nestlings receiving higher average food delivery rates (Table 3).

Given that uni-parental and bi-parental care nests presented similar parental efforts per nestling, I investigated whether this resulted in similar nestling conditions. The mean nest nestling condition did not differ between female-only and bi-parental care broods at 5 d of nestling age (ANOVA, $F(1,40) = 0.03$, $p = 0.86$).

Clutch size was similar in both types of nests (ANOVA, $F(1,39) = 0.95$, $p = 0.34$). Uni-parental care nests had fewer broods of hatchlings (ANOVA, $F(1,39) = 9.26$, $p < 0.005$, uni-parental nests 3.11 ± 0.31 and bi-parental nests 4.06 ± 0.14

nestlings per nest) and 5-d-old nestlings (ANOVA, $F(1,40) = 6.10$, $p < 0.02$, uni-parental nests 2.56 ± 0.38 and bi-parental nests 3.58 ± 0.19 nestlings per nest) (Fig. 1).

Comparison of results on the breeding success parameters between the 2 types of nests revealed that only hatching success statistically differed (ANOVA, $F(1,39) = 10.46$, $p = 0.002$); the number of eggs of female-only care nests that did not hatch was significantly higher (hatching success of uni-parental nests was 59.6% and of bi-parental nests was 80.7%). However, as with the other breeding success parameters, female-only cared nests presented slightly smaller average values; breeding success (uni-parental 21.28% ($n = 9$) and bi-parental nest 30.40% ($n = 32$)), proportion of nests with 1 fledged young (uni-parental 55.55% and bi-parental 56.25%), and number of fledglings per nest (uni-parental 2.00 ± 0.31 fledglings per nest and bi-parental 2.72 ± 0.23 fledglings per nest).

Paired versus single nesting females

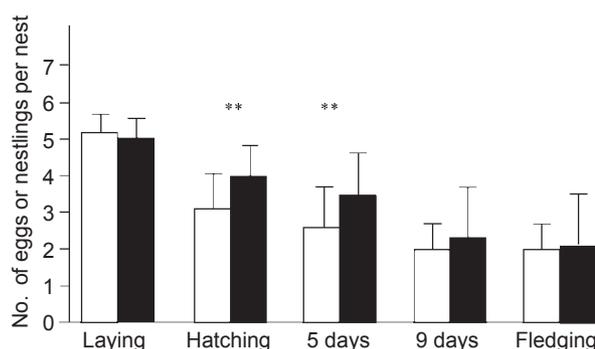


Fig. 1. Number of eggs and nestlings in female-only care nests (white bars) and bi-parental care nests (black bars) during incubation, after hatching, at 5 d old, at 9 d old, and fledglings. **A statistical difference at $p < 0.05$. (Mean \pm SE)

Table 2. Effect of nest parental care pattern and season on parental brooding behavior for the year 2000 (two-way ANOVA multivariate test, patterns Rao $R(3,10) = 2.77$, $p > 0.09$; season Rao $R(3,10) = 0.47$, $p > 0.70$; and pattern \times season Rao $R(3,10) = 0.10$, $p > 0.90$)

	Pattern		<i>F</i>	<i>p</i>	Season		<i>F</i>	<i>p</i>
	Uni-parental nests	Bi-parental nests			Early	Mid		
^a Brooding visit duration (s)	573 \pm 88 (6)	401 \pm 55 (10)	3.8	0.12	505 \pm 68 (7)	434 \pm 74 (9)	1.0	0.33
Brooding visit rate	2.5 \pm 1.3 (6)	4.0 \pm 0.7 (11)	3.2	0.10	4.4 \pm 0.6 (7)	2.9 \pm 0.1 (10)	0.7	0.41
^b Percent of time brooding	41.2 \pm 8.1 (6)	45.4 \pm 8.9 (11)	0.3	0.61	57.2 \pm 7.7 (7)	34.6 \pm 8.2 (10)	1.7	0.22

^aFor ANOVA, values were log ($x+1$)-transformed. ^bFor ANOVA, values were arcsine-transformed.

A multivariate analysis of the female brooding and feeding behavior did not yield a significant effect of year (all $p > 0.10$). However, univariate tests showed differences in some of the parameters of female brooding behavior between years, namely the percentage of brooding time (ANOVA $F(1,35) = 5.2, p < 0.03$) and the duration of the brooding visits (ANOVA $F(1,35) = 4.4, p < 0.05$).

Due to the effect of year on some of the brooding parameters, only nests from the year 2000 were used in the analyses of the effect of season and parental care pattern on the brooding behavior of females. The analysis revealed no effect of pattern or season (Table 4).

In the analysis of the effect of nest parental care pattern and season on female feeding behavior, only the interaction of those factors was significant. Two of the original variables were excluded due to heteroscedasticity; the inclusion of these variables in the analysis produced similar results, and a non-parametric analysis of the effect of pattern and season on female feeding behavior detected no relation.

Although the effects of the 2 factors cannot be considered independent, results of univariate tests suggest that females from uni-parental nests presented different feeding efforts per nestling (Table 5). The analysis of the effect of the nest pattern in female feeding behavior considering only mid-season nests supports this view (ANOVA multivariate Rao test $R(3,22) = 11.02, p < 0.0002$; univariate ANOVA; feeding rate $F(1,24) = 2.77, p > 0.1$; feeding rate per nestling $F(1,24) = 27.4, p < 0.0001$; food delivery rate $F(1,24) = 33.6, p < 0.0001$). Uni-parental females provided food to each nestling more times than did bi-parental females and with higher food load scores/h (Table 5).

The index "female expenditure efficiency",

defined as the ratio between the average care provided to each nestling and the mean nest offspring condition, differed between deserted and paired females when considering the ratio between feeding visit rate per nestling and mean nest offspring condition (Mann-Whitney $U_{9/33} = 63, p < 0.05$; medians: uni = 0.18, bi = 0.10), and the ratio between food delivery rate per nestling and mean nest offspring condition (Mann-Whitney $U_{9/33} = 37, p < 0.05$; medians: uni = 0.38, bi = 0.21). Deserted females had to provide more care to produce nestlings in an average equal condition considering the food delivery rate per nestling (Fig. 2).

DISCUSSION

In bi-parental care nests, male and female feeding behavior did not significantly differ in any of the studied parameters. Overall, no differences

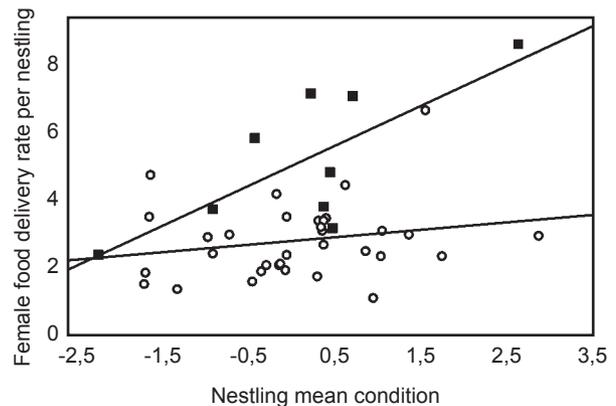


Fig. 2. Variation in the mean nest nestling condition with the female food delivery rate per nestling for uni-parental (squares) and bi-parental care nests (circles) (uni-parental: $F(1,7) = 8.5, r^2 = 0.48, p = 0.02, y = 4.7 + 1.2x$; bi-parental: $F(1,31) = 1.4, r^2 = 0.04, p = 0.24, y = 2.6 + 0.2x$).

Table 3. Effect of nest parental care pattern and season on nestling feeding behavior (two-way ANOVA multivariate test, pattern Rao $R(4,35) = 3.50, p < 0.02$; season Rao $R(4,35) = 2.05, p > 0.10$; and pattern x season Rao $R(4,35) = 2.30, p > 0.07$)

	Pattern		F (1, 38)	p	Season		F (1, 38)	p
	Uni-parental nests	Bi-parental nests			Early	Mid		
Feeding visit rate	4.8 ± 0.8 (9)	8.8 ± 0.7 (33)	7.8	0.008 ^b	7.8 ± 0.9 (16)	8.1 ± 0.8 (26)	0.6	0.44
Feeding visit rate/nestling	2.2 ± 0.3 (9)	2.6 ± 0.2 (33)	3.5	0.07	2.2 ± 0.2 (16)	2.6 ± 0.2 (26)	4.1	0.06
Food delivery rate/nestling	4.9 ± 0.7 (9)	5.4 ± 0.3 (33)	3.0	0.09	4.6 ± 0.4 (16)	5.6 ± 0.3 (26)	7.3	0.01 ^b
^a Load size	2.4 ± 0.2 (9)	2.2 ± 0.1 (33)	3.0	0.09	2.1 ± 0.1 (16)	2.3 ± 0.1 (26)	0.08	0.77

^aFor ANOVA, values were log (x+1)-transformed. ^bAs confirmed with post hoc Tukey's test ($\alpha = 0.05$).

were observed in the major feeding parameters for the different years or between seasons. Each sex's share of the parental expenditure greatly varied between nests. The absence of differences between sexes suggests that males in bi-parental care nests produced feeding efforts similar to those of females. This result supports the view that, in bi-parental species, males escaping parental duties avoid substantial costs, and thus they could possibly increase their future reproductive success (Trivers 1972). For example in Great Reed Warblers, males which had deserted their mates tended to settle earlier the following season and to be polygynous (Urano 1992).

Both sexes exhibited brooding behavior. The fact that females performed more brooding visits and spent more time brooding suggests that the brooding commitment, at least at this nestling age, is sex-biased. Differences between sexes may primarily be due to lack of a brood patch in males. Male brooding behavior appeared to be important to compensate for female foraging absences, especially under adverse weather conditions.

Both sexes showed decreasing values for brooding parameters (percentage of brooding time and brooding visit rate) between early and mid season, which may reflect the effect of an increase

in temperature during spring.

Bi-parental care nests presented a higher total feeding expenditure (both in number of feeding visits and food load score) than did uni-parental nests. However, the average feeding care received by each nestling did not differ between the 2 nest types. Nestlings received similar numbers of feeding visits/h and food load scores/h. This was due to the higher number of nestlings in the bi-parental nests. From these results, one would expect, as observed, that nestling condition was similar between uni- and bi-parental nests. The lack of differences in nestling condition is important since it is known that the probability of survival during the 1st year of life is closely related with body condition at fledging (Perrins 1965, Rinsby et al. 1998). The results suggest that fledglings from uni- and bi-parental nests do not differ in survival probability due to malnutrition at 5 d of age.

Although only hatching success differed between uni- and bi-parental nests, all other breeding success parameters showed the same trend, i.e., slightly smaller values in nests with mate desertion. These results seem to point out a reduction in the fitness payoff of the current reproduction due to desertion, as predicted by Trivers's

Table 4. Effect of type of parental care pattern and season on female brooding behavior in the year 2000 (two-way ANOVA multivariate test, pattern Rao $R(3,10) = 2.07$, $p > 0.16$; season Rao $R(3,10) = 0.69$, $p > 0.50$; and pattern x season Rao $R(3,10) = 0.94$, $p > 0.40$)

	Pattern		F	p	Season		F	p
	Uni-parental females	Bi-parental females			Early	Mid		
Brooding visit duration (s)	573 ± 88 (6)	391 ± 61 (10)	3.1	0.10	520 ± 77 (7)	412 ± 75 (9)	1.2	0.30
Brooding visit rate	2.5 ± 0.5 (6)	2.2 ± 0.4 (11)	0.1	0.73	2.7 ± 0.2 (7)	2.0 ± 0.5 (10)	1.0	0.34
^a Percent of time brooding	41.2 ± 8.1 (6)	24.1 ± 5.0 (11)	2.4	0.15	38.0 ± 3.0 (7)	24.6 ± 6.8 (10)	2.1	0.17

^aFor ANOVA, values were arcsine-transformed.

Table 5. Effect of type of parental care pattern and season on the female feeding parameters (two-way ANOVA multivariate test, pattern Rao $R(3,36) = 2.43$, $p > 0.08$; season Rao $R(3,36) = 2.26$, $p > 0.09$; and pattern x season Rao $R(3,36) = 2.97$, $p < 0.05$)

	Pattern		F	p	Season		F	p
	Uni-parental females	Bi-parental females			Early	Mid		
Feeding visit rate	4.8 ± 0.8 (9)	4.1 ± 0.3 (33)	0.1	0.84	4.3 ± 0.5 (16)	4.3 ± 0.3 (26)	0.7	0.39
^a Feeding visit rate/nestling	2.2 ± 0.3 (9)	1.2 ± 0.1 (33)	3.4	0.07	1.3 ± 0.1 (16)	1.5 ± 0.2 (26)	6.5	0.01 ^b
^a Food delivery rate/nestling	4.9 ± 0.7 (9)	2.7 ± 0.2 (33)	6.9	0.01 ^b	2.6 ± 0.3 (16)	3.5 ± 0.3 (26)	6.8	0.012

^aFor ANOVA, values were log (x+1)-transformed; ^bAs confirmed with post hoc Tukey's test ($\alpha = 0.05$).

(1972) mate desertion hypothesis. Other studies of altricial species with facultative mate desertion have reported minimal consequences on the reproductive success of deserted nests (Beissinger 1987, Ezaki 1988, Urano 1992) and contrast with results in studies with polygynic species (e.g., Harvey et al. 1988, Pinxten and Eens 1990) or with male removal experiences (as reviewed in Møller 2000). The absence of a clear trend could have been due to the small sample size of uni-parental nests with success in this study or due to some confounding variable such as the quality of the deserted females that may have affected the correct assessment of the costs of desertion.

Females from uni-parental nests presented similar total parental care expenditures as compared to bi-parental females. This may have been due to the smaller number of nestlings at the time of observation. However when parental expenditure per nestling was analyzed, we found that single female on average provided almost twice as much per nestling, i.e., a female had to invest more in order to feed the same number of offspring. This difference suggests that single female compensate for the absence of male parental care to avoid a reduction in offspring fitness, a behavior that has been also described in Great Reed Warblers (Ezaki 1988), in Zebra Finches (*Taeniopygia guttata*) (Royle et al. 2002), and in Magnificent Frigatebirds (*Fregata magnificens*) (J. L. Osorno, pers. comm.). In doing so and according to the predictions of Trivers (1972), this extra effort should result in an increase of the cost of the current reproduction which may affect female fitness (Bryant 1988, Gustafsson and Sutherland 1988).

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