Egg burial in penduline tits, *Remiz pendulinus:* its role in mate desertion and female polyandry

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One important component in the mating strategy of an already-mated individual is the decision to remain with the partner and care for the offspring or to desert. Almost all research on nest desertion has focused on the costs and benefits of continued parental care versus desertion of both parents. However, if it pays both parents to desert, the timing of desertion is most important. In birds, where all eggs are fertilized well before the last egg is laid, males should be the first to desert. Even if females try to hide their fertile period, it is likely that the appearance of eggs acts as a cue that males can use to calculate the timing of their desertion. Here we examine egg burial behavior in penduline tits and its possible effects on parental behavior and desertion. Penduline tits perform uniparental care from the earliest point of breeding, and both sexes try to become polygamous. We found that 36% of investigated males were polygynous and deserted as soon as the first egg appeared in their nest, and 12.5% of females became polyandrous. About 27% of the nests were deserted by both sexes, which means high costs for females in terms of wasted energy in eggs and for males in terms of wasted energy and time in building elaborate nests. Females cover the eggs, and several facts indicate that egg covering is a deceptive behavior of females: (1) females cover the eggs in the morning before leaving the nest for the first time, (2) females are more aggressive toward their mates during the laying period than before laying, (3) females try to prevent males from entering the nest when eggs have been experimentally uncovered, and (4) females uncover the eggs as soon as males are experimentally removed. Finally, we found that a female can only desert the nest before the male deserts when she covers the eggs. We conclude that the higher the proportion of eggs a female can hide, the greater her chance of becoming polyandrous. *Key words:* egg burial, female strategy, mate desertion, penduline tits, polyandry. *[Behav Ecol 8:20–27 (1997)]*

E gg burial behavior of females during the laying phase is common in several bird species (reviewed in Champhell and Lack, 1985; Welty and Baptista, 1988). Cases where eggs are covered by nest material (Hohn, 1993; Keller, 1989) or actively buried in the nest base (Briskie and Sealy, 1988; Clark and Robertson, 1981; Haftorn, 1981) have been described. This behavior may have the function of reducing predation (Broeckhuysen and Frost, 1968; Keller, 1989) or thermoregulating eggs (Bochenski, 1961). Some authors (Briskie and Sealy, 1988; Clark and Robertson, 1981; Petrie and Møller, 1991) have suggested that egg burial may be a response to brood parasitism. In hole-nesting species with large clutches, where females sleep inside the nest cavity during laying, egg burial may also function to reduce hatching asynchrony (Kempenaers B, personal communication).

Here we focus on the function of egg burial behavior during the fertile period in relation to later parental behavior in the polygynandrous penduline tit, *Remiz pendulinus.* Penduline tits seem to be a suitable study subject because (1) they build elaborate pendulous nests where eggs are buried in the soft material of the nest base during the fertile period (see Burckhardt, 1948; Steinfatt, 1934), (2) they perform exclusive uniparental care by which either sex can rear a brood alone from the earliest point in the nesting cycle (Schönfeld, 1994), and (3) nest desertion occurs frequently (Franz, 1991; Hoi et al., 1994,1996; Persson and Öhrström, 1989). Usually it is the male who deserts, but there are also cases of nest desertion by females (Persson and Öhrström, 1989). An earlier study

(Franz, 1991) showed a polygyny rate of 25% and a polyandry rate of 12% in the area we chose for investigation.

Hypotheses explaining nest desertion have mainly focused on (1) fitness costs and benefits for continued parental care and desertion (e.g., Dawkins, 1976; Grafen and Sibley, 1978; Lazarus, 1990; Maynard Smith, 1977; Pienkowski and Greenwood, 1979), (2) effects of various environmental variables on these costs and benefits (e.g., Emlen and Oring, 1977; Graul et al., 1977; Pitelka et al., 1974), and (3) the possibility that individuals acquire multiple mates (Beissinger, 1986; Beissinger and Snyder, 1987; Boucher, 1977; Trivers, 1972). Maynard Smith (1977) pointed out that the timing of desertion may be important if it pays both parents to desert. Even when either sex can rear a brood alone from the earliest point in the nesting cycle, males should be the first to desert because all eggs are fertilized well before the last egg is laid. Thus, a male may desert a female before the clutch is complete, putting his mate in a "cruel bind" (Trivers, 1972). Females are at a disadvantage in this case because they must be the last parent present with the clutch. Even if females could hide their fertile period, it is likely that the appearance of eggs acts as a cue that males can use to determine their female's fertile phase (Birkhead, 1982; Møller, 1987) and hence to start attracting additional mates (Hasselquist and Bensch, 1991; Pinxten et al., 1987).

Because females would benefit by deceiving their mates during the egg-laying period, we wanted to investigate if egg burial behavior in penduline tits may be a mechanism by which females could increase their chances to desert before the male deserts and hence become polyandrous. This deception basically requires that females bury eggs. If egg burying is a deceptive behavior of females, several predictions can be made: (1) Females should attempt to keep males out of their nests. In line with this prediction, we would expect an increase in

aggressive behavior toward male mates during egg laying, especially in cases where females are not able to bury their eggs perfectly. (2) Eggs should be buried from start of laying and for as long as the female can hide them. We would not expect an interruption in hiding (either in daily or seasonal patterns) before leaving the nest. (3) Egg burying should stop and uncovering of eggs should start after the male has deserted the nest. (4) Egg burial by females should allow them to desert before the male, which in turn should increase females' probability of becoming polyandrous.

We examined the specific time pattern of egg burial during the egg-laying sequence to test the following alternative predictions for the nest predation, thermoregulation, and hatching asynchrony hypotheses. First, if egg burial in penduline tits is related to nest predation, one would expect females to adjust their behavior to the relative brood value; i.e., cover eggs more with increasing clutch size (Broekhuysen and Frost, 1968; Keller, 1989). Females should also cover eggs before leaving the nest to forage during incubation (Broekhuysen and Frost, 1968; Haftorn, 1981; Keller, 1989). As clutch size increases, one may expect at least part of the clutch to be covered given a possible space constraint.

Second, if egg burial is related to weather conditions, we predict no specific time pattern with regard to clutch size during one egg-laying sequence but a general seasonal decline of egg burial behavior due to more predictable and generally good weather conditions late in the breeding season. Also, we predict egg burial during adverse weather conditions before incubation breaks during the day.

Finally, if egg burial reduces hatching asynchrony, we predict the same time pattern in egg burial as expected for the male deception hypothesis. However, only for the male deception hypothesis do we predict that eggs will be uncovered after the male deserts.

METHODS

Study site

We studied penduline tits during the breeding seasons of 1992–1994 at two different study sites about 60 km from Vienna, Austria: a wet forest area along the March River (48°16′N, 16°57′E) and the region around Lake Neusiedl (47°46′N, 16°48′E). These areas are 80 km apart. The wet forest area is dominated by trees, mainly willows (*Salix* spp.) and poplars (*Populus* spp.), interspersed with water enclosures surrounded by small marshes or meadows. Much of the area around Lake Neusiedl is characterized by open landscapes, dominated by an extended marshy area. Trees (willows and poplars) only occur along the dry edge of the reed belt and along causeways leading into the reeds.

Study species

Penduline tits weigh about 9 g and are the only European species in the family Remizidae. They show a slight sexual dimorphism in the extension of the black forehead (Glutz von Blotzheim and Bauer, 1994; Schönfeld, 1994), so observers can sex adults with the aid of binoculars. Males build elaborate pendulous nests to attract females (Franz and Theiss, 1983). They place their nests on the extreme outer branches of the tree crown (mainly willows and poplars), 2–20 m above the ground. Males start to advertise at the beginning of the nest-building phase by means of song and calls. Female mate choice seems to be mainly based on nest features important for thermoregulating eggs (Hoi et al., 1994). After pair formation, females take over the majority of nest building and are mainly responsible for the construction of the inner part

(bottom layer) of the nest (Glutz von Blotzheim and Bauer, 1994; Schönfeld, 1994). The warm, stable microclimate in this type of nest may have influenced the evolution of single-parent incubation, allowing the second adult to pursue additional breeding attempts (Hoi et al., 1994).

Males started nest building in the first week of April, and broods were initiated (first egg) from 16 April to 8 July. Modal clutch size was 5 eggs (range 2–8 eggs, *n* = 153 clutches).

Censusing and behavioral observations

We caught most males and females during nest building, before egg laying, by mist-netting, using playbacks of songs and calls and old nests or nest material to attract them. All birds were individually color-ringed for individual recognition. Observational data were gathered from 1992 to 1994, and no individual was used more than once in data analyses.

We made behavioral observations before and during egg laying, starting with the date when the female participated in nest building for the first time. During this period we visited each nest (*n* = 144) only once a day between 0700 h and 1000 h local time (0500 h–0800 h GMT) on a regular basis to record appearance and position of the eggs. We distinguished three different types of egg position: completely covered eggs (no eggs on the surface of the nest base), partially covered eggs (part of at least one egg prominent), or no eggs covered. The eggs were checked by probing the inside of the nest with fingers. In this way it is easy to detect the three different types. When in doubt, we used both hands, one holding the bottom of the nest and the second detecting the buried eggs with the fingers by applying slight pressure against the bottom.

We performed 20-min behavioral observations three to five times a day using one 0-time sampling in 30-s intervals from a distance of 20 m. Additionally, the frequency of different behaviors was recorded for each sampling interval. Simultaneously active nests were watched in a rotating schedule to avoid watching individual nests at the same time each day. We recorded nest-building activity, aggressive interactions between partners at or near the nest, and male and female arrivals near (within 10 m) or at the nest and departure times in order to calculate the nest attendance for both pair members. The date the male (or female) was seen for the last time was considered as the time of desertion.

To find out whether it is the female who buries the eggs, we checked the nest (*n* = 6) twice a day. Since females sleep in the nest during the laying phase, we checked nests of laying females at night (2200 h) and subsequently in the early morning (0400 h–0600 h) just after the female had left the nest for the first time and before the male could enter.

Possible effects of repeated nest visits on nest desertion

When discussing the adaptive significance of nest desertion by small birds, it is important to show that desertion is not simply the result of disturbance caused by repeated nest visits of field-workers, including climbing the tree and touching eggs and searching in the nest lining. In penduline tits, desertion by males, females, or both sexes occurs naturally (Franz, 1991; Persson and Öhrström, 1989; Schönfeld, 1994). Desertion as a result of disturbance can be excluded for several reasons. Franz (1991) investigated penduline tits in the same study area and found a similar number of nests attended by females or males but a higher rate of completely deserted nests, although he did not visit the nests during the fertile period.

Comparing the number of nests deserted by both sexes and the number of nests attended by males or females between nests never visited during the laying phase (28 attended by male, 69 by female, 24 deserted by both sexes) and nests re-

peatedly visited during the laying phase (15 attended by male, 45 by female, 18 deserted by both sexes), we found no significant difference ($\chi^2 = 0.57$, df $= 2$, $p = .749$), so the relative frequency of each type of nest is the same for disturbed and undisturbed nests.

Also, comparing the number of nest visits during laying and before desertion for each type of nest, we found no difference in the intensity of disturbance among the three types of nests (Kruskal-Wallis test, $t = 1.3$, df $= 2$, $p = .59$). Thus, it seems unlikely that disturbance of nests influences nest desertion or differently affects male and female behavior.

Treatments and experiments

To get experimental support for the occurrence of female egg burial behavior, five randomly selected nests were experimentally manipulated by uncovering the eggs by hand twice a day (0700–0900 h and 1500–1700 h). These manipulations were performed either on day +1 or day +2 of egg laying, day 0 being the day when the first egg was laid. We checked manipulated nests after the male or female had visited the nest again.

If egg burial is a deceptive behavior by females, a female should aggressively prevent her mate from checking the nest and thereby discovering the eggs. We would therefore predict that female aggression toward her mate should occur more often during egg laying than before egg laying, after removing the inner lining of the nest, and uncovering the eggs. To test these predictions, we recorded female aggressive behavior (attacks, chases at the nest entrance) toward the male mate over 20-min periods. We compared data on female aggressive behavior before (day −4 to −1) and during egg laying (day 0 to day +3) and in manipulated nests just before egg uncovering (observations started about 30 min before egg manipulation) and after eggs were experimentally uncovered (observation periods started when the female appeared at the nest entrance for the first time).

We performed male removal experiments to examine the idea that egg burial is related to male presence. Males of six randomly selected nests with covered eggs were mist-netted on day 0 and day +1 and held in aviaries until the female started incubation. We checked the nests at 2-h intervals to see whether the eggs were still covered. All experiments were done in 1994.

Statistical analyses

We used parametric tests when the assumption of normality was met. Tests are two-tailed unless otherwise indicated. The power of the experimental treatments was increased by performing directional, one-tailed tests instead of two-tailed tests. We did this when there was a clear directional prediction. To test whether experimental uncovering affects male desertion, we used a conditional binomial exact test (Rice, 1988) because this test, in contrast to Fisher's Exact test, accommodates different levels of a priori information about the underlying probability. Therefore, we compared the experimentally induced probability of male desertion with the expected probability of male desertion for each day of egg laying for a total of 141 nests without manipulation. We carried out egg-uncovering experiments on day +1 and +2. We calculated male desertion for day +2 as $p = .26$ for the remaining 99 nests for that day. At day +2, the probability of desertion is higher than at day +1 ($p = 0.19$ for 123 nests); therefore, the use of the higher probability level of day +2 for testing experimental versus expected probabilities produces more conservative results.

To test whether egg uncovering is increased by experimen-

tal removal of males, we compared the experimentally induced probability of egg uncovering with the expected probability that egg uncovering occurs naturally for each day using a conditional binomial exact test (Rice, 1988). We carried out removal experiments on day 0 and day +1, and eggs were uncovered at the latest on the following morning (day +2). We calculated the expected probability of egg uncovering for day +2 for 30 nests as $p = .51$. Again, when using day +2 for testing experimental versus expected probabilities, the comparison produces more conservative results than when using day 0 ($p = .16$ for 50 nests), or day +1 ($p = .24$ for 42 nests).

We checked 144 nests several times during the laying period to investigate if there is any pattern of egg burial related to the number of eggs laid. This data set includes first as well as later broods. To avoid the effect of a possible seasonal pattern in egg burial behavior (i.e., a decreasing trend in egg burial during the laying period, which could lead to a decrease in the sample size for cases of burial for nests with increasing clutch size), 33 nests were checked daily during the whole laying period, and a repeated-measures ANOVA was used to check if the laying sequence affects the probability that eggs are buried. The dependent variable was the arcsine-transformed proportion (all or none) of eggs buried during each day of the laying period.

To calculate the proportion of male or female attended broods and nests that are deserted by both parents, we also included data from 1995. This calculation is therefore based on 223 nests.

RESULTS

Egg burial

During the laying period, egg burial was a common event in penduline tit nests (Figure 1). One important characteristic of this egg burial behavior is that all eggs are usually buried from the first egg until the day when all eggs are uncovered; for example, if a female with a clutch of five eggs buries three eggs, that means the first egg is buried on day 0, the first and the second egg are buried on day +1, and three eggs are buried on day +2. From day +3 on, all eggs are uncovered. If this female were to only bury one egg, then only the first egg would be buried on day 0. After uncovering, eggs have been never observed to be buried a second time. We found one or more buried eggs in 86% of nests ($n = 144$). Egg burial showed a temporal pattern, such that the frequency of nests with buried eggs decreased over the egg-laying period (Figure 2). The first egg was buried in almost 80% of nests, but on day 3, as many as 30% of the nests had all four eggs buried. A repeated-measures ANOVA on 33 nests, which were checked daily, revealed a significant increase in the likelihood that all eggs are uncovered along the laying sequence ($F = 13.43$, df $= 5,35$, $p<.00001$). Females laid one egg per day, on average 5.24 ± 0.15 (SE) eggs ($n = 72$ clutches). After the fourth day of laying, buried clutches were observed only rarely (Figure 2). The median time that a clutch was buried was 2.5 days (interquartile range $= 2$–4, $n = 19$ clutches). In rare cases, eggs were only partially covered by the nest material, and these cases were excluded from further analyses.

Do females bury eggs?

Circumstantial evidence for the assumption that eggs are buried by females is provided by their role in nest building. In the course of nest building, females increased their effort, and during the final stage they dedicated 100% of their time in the nest to working in the incubation chamber (see also Beitz, 1985). During this period females also started sleeping inside the nest at night.

Figure 1
View of entire nest (left), view of sagittal section of nest (middle), showing buried eggs (arrow), and schematic cross-section of a nest showing three buried eggs.

Direct evidence for egg covering by females was gathered by checking nests during the night and early in the morning during the first days of egg laying. Nightly checks of six nests during the first 3 days (day 0 to day +2) revealed that the eggs were not covered during the night and that the females slept on them. Checking the nests after the females had left them for the first time the following morning and before males could have entered revealed that all of the eggs were

Figure 2
Proportion of nests with covered (filled area), uncovered (open area), and partly covered eggs (hatched area) in relation to start of egg laying (day 0 is the day when the first egg is laid). Number of nests is given above bars.

covered. Once eggs were buried they usually remained covered for the rest of the day.

In all cases where eggs were experimentally uncovered twice during the day (two trials at five nests), females covered them again shortly after arriving at the nest for the first time.

Relation between male desertion and uncovered eggs

There was a significant correlation ($r = .78$, $p < .0001$, $n = 19$) between the number of days a male stayed at the nest during the laying period and the number of days a female kept her eggs buried (Figure 3). In most cases, the males deserted on the same or the following day when the female uncovered the eggs, and only in two cases did the male disappear before that day (Figure 3). For both cases we cannot exclude that the male was predated. Detailed observations at seven nests revealed that males deserted on average 5 h $\pm$ 1 (SE) after the eggs became visible. In those cases where we experimentally uncovered the eggs, four out of five males deserted (on the same day). This is significantly more than expected for unmanipulated nests for the day of egg laying when we did the experiments (conditional binomial exact test, one-tailed; $p = .009$). In the one case where the male stayed, the female had been able to quickly cover the eggs again, and she also tried to prevent the male from entering the nest (see below), so he probably had no opportunity to check the nest for eggs.

Thus, males deserted as soon as eggs appeared in the nest. In 15.4% of the unmanipulated nests, the first egg was uncovered (see Figure 2) and about 12.7% males also deserted that early (see Table 1). Male desertion is most frequent on day +2.
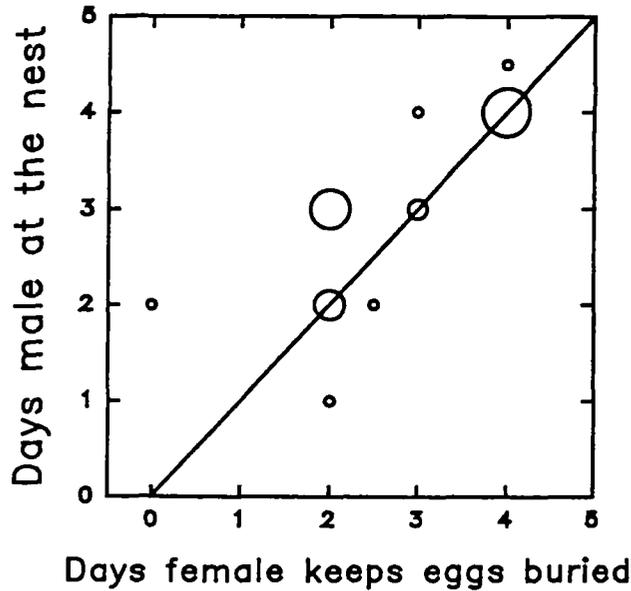
Clutches attended by males were significantly smaller [$\bar{x} = 4.2 \pm 0.25$ (SE), n = 24] than those attended by females [$\bar{x} = 5.8 \pm 0.13$ (SE), $n = 43$, t test, $t = 5.65$, $p < .0001$].
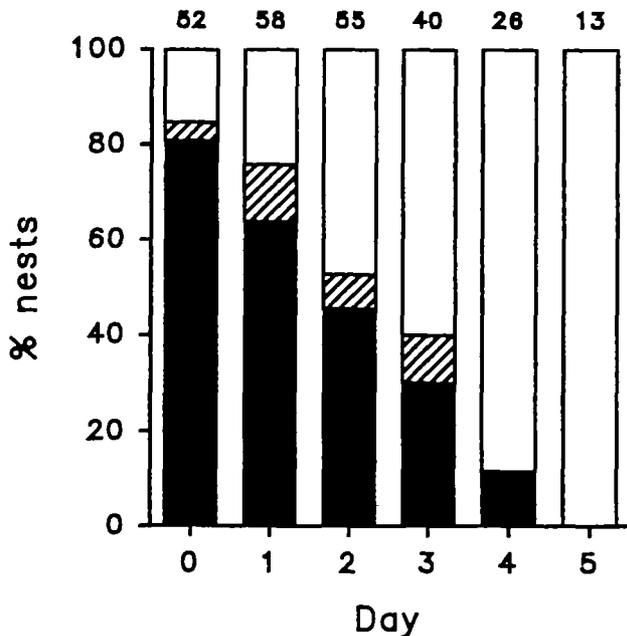
Egg covering as a female strategy for polyandry?

We examined the aggressive behavior of females toward their male partners when the male apparently tried to enter the nest. The results (Figure 4a) show that females were signifi-

Figure 3
The number of days a male stays at the nest in relation to the number of days the female keeps her eggs buried (n = 19 nests). The straight line indicates the time when a female unburies her eggs. The symbols indicate one (smallest circles) to five (biggest circle) nests per symbol.

Table 1
The percentage (absolute number) of males and females that deserted for each day in the laying cycle for 141 nests

Day in laying cycle	Male deserts	Female deserts
0	12.7 (18)	4.2 (6)
+1	19.5 (24)	10.4 (14)
+2	26.3 (26)	20.7 (25)
+3	31.5 (23)	29.2 (28)
+4	0.02 (1)	8.8 (6)
+5	0	3.0 (2)

a)

b)

cantly more aggressive during egg laying than during prelaying (binomial test, $p < .005$, n = 11 nests).
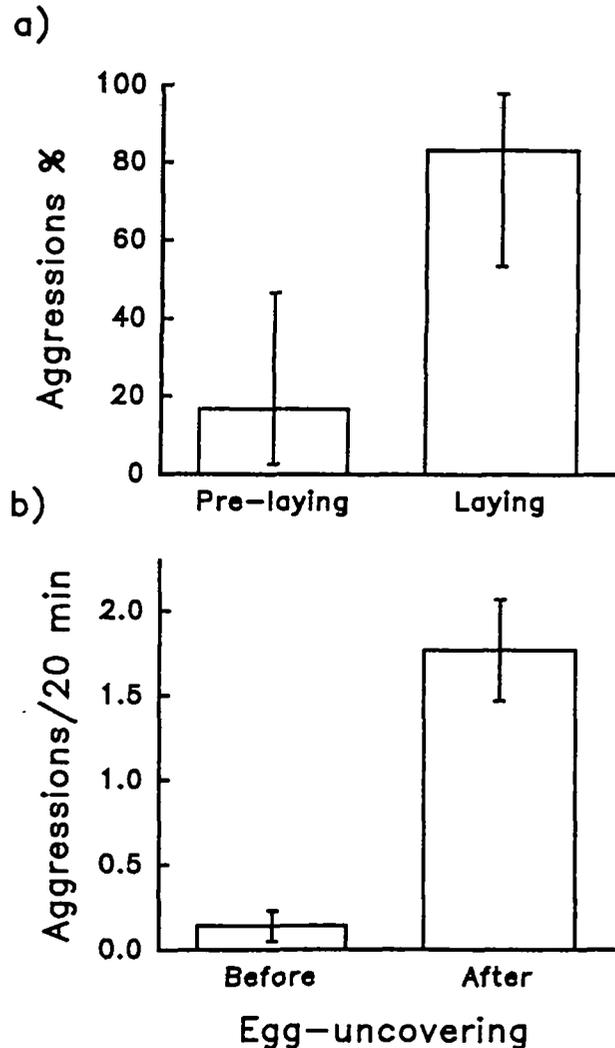
Females were also significantly more aggressive toward their males when eggs were experimentally uncovered (Wilcoxon matched-pairs signed-ranks test, $z = 2.02$, $p = .04$, n = 5 nests; Figure 4b). Pooling the information for experimentally manipulated (n = 5) and nonmanipulated nests (n = 11) revealed that only 2 (3.9%) of 51 aggressive attacks by the female were ineffective in preventing the male from entering the nest. In comparison, in those cases where the female was not aggressive or absent, 138 (78.4%) of 176 male arrivals at the nest ended with the male entering the nest.

Further, experimental removal of males during day 0 and day +1 revealed that in three cases females uncovered the eggs 5 h, 5 h, and 8 h after the male had been removed, and in three more cases females stopped covering them the next morning. Thus, egg uncovering occurs significantly more often than expected for unmanipulated nests for that day (the probability of egg uncovering for unmanipulated nests on day +2 is $p = .53$) during egg laying (conditional binomial exact test, one-tailed, $p<.005$). The temporal pattern of female desertion in relation to egg laying showed a peak on day +3 (see Table 1).

To test whether egg burial affected the probability of becoming polyandrous, we compared nests with carefully covered eggs (including those nests where at least the first egg was covered) and without any covered eggs (no eggs covered from day 0 onwards). None of 13 females was able to retain the male to attend the brood if no egg was covered, but 14 of 50 females were successful if at least one egg was covered (Fisher's Exact test, $p = .025$). The proportion of covered eggs per clutch was significantly higher in cases where the males attended the brood (Mann-Whitney U test, $z = 3.3$, n = 10,19, $p<.001$; Figure 5). We observed cases of polyandry (where the female was successively mated with a second male) in 5 of 40 ringed females (12.5%). This might be a minimum rate of polyandry; it is hard to follow females because breeding at-

Figure 4
Aggressive actions of females against their mates when the mates tried to enter the nest (a) during the prelaying (day −6 to day −1) and laying period (day 0 to day +4); given is the number of aggressive actions occurring during each period as a proportion (95% confidence intervals) of the total number of observed aggressive actions (n = 18 aggressive actions by the female for 11 nests), and (b) before and after experimental egg uncovering; given is the mean number of aggressive actions (± SE)/20 min. Experiments were done on 5 nests from day 0 to day +4 including 33 aggressive actions by the female (see Methods).
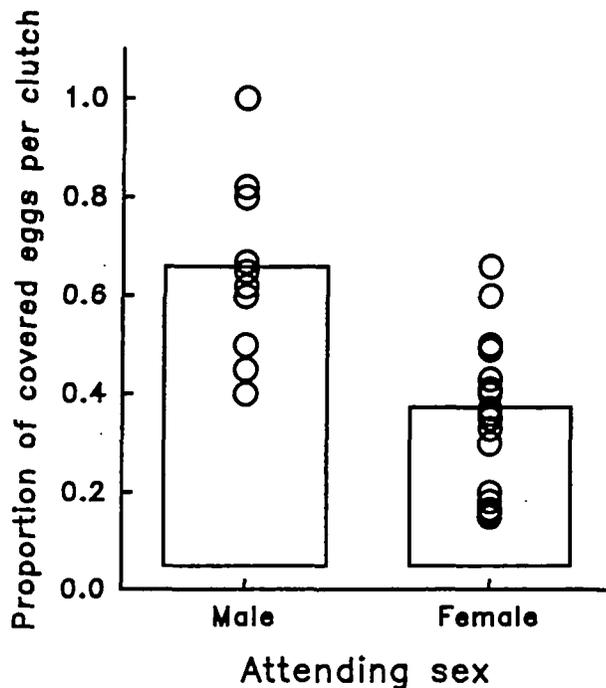
Figure 5
The proportion of previously covered eggs (of total clutch size) for broods attended by males or by females. Given are means (bars) and individual cases (open circles).

tempts within one breeding season can take place more than 200 km apart (Franz et al., 1987). Of 223 nests, 44 (19.8 %) were attended by the male alone. Additionally, in 61 of 223 nests (27.3%), both the male and the female deserted the nest. These complete desertions may include cases where females tried to be polyandrous but were not successful. However, we found that desertion by both sexes was more likely if the first two eggs remained uncovered (binomial test, $p < .05$, $n = 19$). Most nests, however, were attended by the female alone (53%, $n = 118$ nests), and at least 18 out of 50 ringed males (36%) managed to attract one or more additional mates.

To look for a seasonal trend in the identity of the incubating sex, we ranked nests according to the start of egg laying. We compared ranks among female- and male-incubated clutches and deserted nests. However, we found no differences (Kruskal-Wallis test, $H = 0.01$, df $= 2$, 117, $p > .9$), so there seems to be no seasonal effect influencing which sex incubates the eggs.

DISCUSSION

Our results on egg burial behavior in penduline tits do not obviously support any of the hypotheses that are commonly used to explain egg burial behavior in birds (Broekhuysen and Frost, 1968; Keller, 1989; Petrie and Møller, 1991), but we cannot exclude that penduline tits may draw at least some benefits of this egg burial behavior that are related to these hypotheses. We can also not exclude that one of these benefits might be the original (historical) reason for the evolution of this behavior, such as to prevent eggs from rolling out of the pendulous nests (Burckhardt, 1948; Steinfatt, 1934; Valera F, et al., personal observation). Because strong winds, for example, can cause eggs to be hurled out of the nest (Valera F, et al., unpublished results), we would expect egg burial to be

related to the weather, specifically to strong winds, and not to laying order. Furthermore, egg burial occurs during the entire breeding season, even though weather conditions change during the season.

A functional role for egg burial in reducing the risk of nest predation seems to be less important because nest predation is generally low in this species (Schönfeld, 1994), and there is only one specialized predator, the great spotted woodpecker, *Picoides major* (Dittberner and Dittberner, 1991; Valera F, et al., unpublished data), which preys upon nests mainly during the chick stage. In species where egg burial may serve to reduce predation (e.g., great crested grebes, *Podiceps cristatus*, black-necked grebes, *Podiceps nigricollis*, see Broeckhuysen and Frost, 1968; Keller, 1989), egg burial also occurs during incubation breaks, which is not the case in penduline tits. Additionally, we would expect females to cover eggs more, the more eggs they have to lose (Broekhuysen and Frost 1968; Keller, 1989) or at least try to bury part of the clutch.

Several authors (Briskie and Sealy, 1988; Clark and Robertson, 1981; Petrie and Møller, 1991) mention egg burial as a means of avoiding egg parasitism. Intraspecific nest parasitism does occur in penduline tits (Valera F, et al., unpublished data). Egg burial may be an efficient strategy to avoid nest parasitism because a parasitizing female should not lay her egg in an apparently empty nest (the parasitic egg would be easily detected or the parasitic female would need a lot of time and effort to bury the egg, which is unlikely). The relationship between egg uncovering and male desertion, the results of the male removal experiment, and the increase in female aggression against her mate when eggs are experimentally uncovered, however, cannot be explained by nest parasitism or predation. Neither the weather, nest predation, nor the nest parasitism hypothesis can explain the observed temporal pattern of egg burial. One explanation might be the prevention of hatching asynchrony, as females sleep in the nest. Thus burial of eggs could prevent unequal incubation. But this explanation also cannot explain the relationship between egg uncovering and male desertion or the result of the male removal experiment. Furthermore, nightly checks showed that females uncover the eggs and actually sleep on them. In addition, asynchronous hatching is common in our population (Valera F, et al., unpublished data).

In the penduline tit, either sex may desert the brood during the egg-laying period (Schönfeld, 1994). Which sex deserts is strongly influenced by the male detection of eggs during laying and hence female egg burial behavior. In this species, therefore, manipulation of information may be one option to alter the "cruel bind" of females (Dawkins, 1976; Trivers, 1972). The results offer direct observational and experimental evidence that it is the female who buries the eggs. The data further show that males desert soon after they recognize the presence of eggs in the nest. That egg burial is a deceptive behavior (i.e., females bury the eggs to hide information from males) is supported by the fact that females uncover their eggs after the male deserts, which was also tested experimentally by removing males. Further support for the male deception hypothesis is provided by the following observations: (1) female aggression directed toward the male was most intense during egg laying; (2) after experimentally uncovering the eggs, female aggression at the nest entrance increased and succeeded in preventing the male from entering the nest; and (3) eggs were covered by females from the start of laying and stayed buried as long as the female could hide them. We did observe only few cases where the egg(s) appeared uncovered and some hours later they were again well covered. In all these cases the female finally attended the brood. Usually the female did not bury the eggs again after she had stopped burying eggs for 1 day (e.g., two eggs unburied and three eggs

again buried). Finally, we found that this behavior is an important tactic for the female to increase her probability of becoming polyandrous, and this probability increases with the female's ability to cover eggs and deceive the male.

One might ask why males do not look for buried eggs. However, males are not supposed to be aware that egg laying has begun, so they do not look for something which they do not expect to exist (this is easier to imagine for inexperienced males). Males seldom build in the incubation chamber, and the females clearly show that they do not like the male to enter the nest. Furthermore, the males have to forage, look for extrapair copulations (see Birkhead and Møller, 1992), and guard the mate as well as the nest (Schleicher et al., 1993). Males do go into the nest, but if the eggs are well buried and they do not expect that there is something inside, why should they remove the inner part which has been perfectly prepared by the female?

In recent years, several studies have shown that females have behavioral and physiological mechanisms to control paternity (Birkhead and Møller, 1993; Gowaty, 1994, 1995). Behavioral mechanisms have been mainly related to the timing of copulations with different males. In line with this, egg-covering behavior during the fertile phase can also be seen as one of a variety of different strategies by which females can resist male control of paternity.

If females have developed this behavior to gain an advantage over the male, why do not all females become polyandrous? One explanation might be that the probability a male will discover the eggs is also high for buried eggs and might increase with the number of eggs a female keeps hidden. This is indirectly supported by the fact that clutches incubated by males were significantly smaller than those incubated by females. Whether a male detects buried eggs might depend on his age and experience. Females seem to face a trade-off between deserting the male with a small clutch or trying to bury as many eggs as possible but risking discovery by the male and his subsequent desertion. However, we observed three cases where females buried few eggs and deserted, but returned on subsequent mornings to lay additional eggs during the longer morning incubation breaks of the males. But even in this case, the female must be careful because the male may desert if he realizes that the female is near the nest. We had two such additional cases with the result that the nest was deserted by both parents.

There were some nests in which females made no attempt to bury eggs. This might be due to the fact that these were young, inexperienced females. However, there were no significant differences in the mask length or width of these females, which suggests that they were not younger than average (Valera F, et al., unpublished data). Another explanation could be that females may consider the partner's strategy (Lazarus, 1990). If there are clear indications that the partner will desert, for instance, because of a biased sex ratio, the time in the breeding season, or food availability, females may not use the egg burial strategy. According to Burley's differential allocation hypothesis (1988), one could imagine that females are "selected" to stay and attend the brood, especially when their partners are very attractive males.

However, those females trying to hide their eggs also have behavioral mechanisms to strengthen the effectiveness of egg burial. Several authors have reported that females become aggressive to their mates after nest completion and during laying (Boitz, 1964; Franz and Theiss, 1983; Persson and Öhrström, 1980) and concluded that they try to chase males away from the nest so that it will not be disturbed. Our results, however, suggest that this aggression is part of a female's tactic to prevent the male from detecting the eggs. One might argue that the male could use female aggressiveness as an indicator of

egg laying and that he should desert if the female prevents him from entering the nest. However, aggressive interactions are rather infrequent (only 18 aggressive interactions by 11 females against their mates were observed for 144 nests) and, especially in those pairs where eggs are well buried, no aggression occurs at all. Since females also attack nonmate males, mates could interpret infrequent attacks directed toward them as female nest defense. Furthermore, if males used increased aggressiveness of females near the nest as a cue for laying status, females in turn could avoid this by always being aggressive.

Penduline tits are the only small passerine species where such a system of ambisexual polygamy occurs (Persson and Öhrström, 1989). The nest seems to play a major role in this unique mating system due to its special characteristics: the high insulation capacity, which facilitates uniparental care, the importance of the nest in the mate choice process (Hoi et al., 1994), and the nest material, which offers the possibility of egg-covering behavior.

This study provides the first experimental evidence that manipulation of information can be one useful way to get out of the "cruel bind" normally faced by females (Dawkins, 1976; Trivers, 1972;). In penduline tits, males and females can care equally well for offspring (Schönfeld, 1994). Our results show that both sexes seem to have opportunities to mate again successfully after deserting the first partner. The timing of desertion is one important determinant of who will desert and who will take care of the brood. The relative quality (experience) of the two combatants in this battle of the sexes is likely to greatly influence the outcome of each decision whether to desert or to care. The outcome should also be influenced by experience, such as age, number of times deserted, and variation in female egg burial behavior. Furthermore, the operational sex ratio is likely to change during the season (Franz, 1991) and across years (Valera F, et al., personal observation) with strong implications for future reproductive opportunities, which will differ across the sexes. This is supported by observations that males are more likely to care for young late in the season when the time available for nest building becomes a constraint (Franz, 1991). However, one should point out here that, even if there are no further mating options available, there might be instances for both sexes where desertion could be advantageous because they can start to moult earlier or avoid costs of incubation and feeding.

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