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# Infanticidal and anti-infanticidal strategies in the swallow *Hirundo rustica*

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**Summary.** Five definite and nine suspected cases of infanticide were documented in the swallow *Hirundo rustica*. Unmated males visited neighbouring nests and removed entire broods during the first days of the nestling period, preferentially from nests owned by young late-breeding individuals. Infanticide followed the disappearance of the male nest owner in 11 of the 14 cases. The unmated infanticidal male later mated with the female victim although renesting during the same season only took place in 12 of the 14 cases. The fraction of unmated males increased with colony size, and infanticide was relatively more common if unmated males were abundant. Females did not engage in extra-pair copulations in order to avoid infanticide. Intense guarding of the nest and its contents prevented infanticide. Nest guarding intensity was higher in colonial compared with solitarily breeding swallows, and guarding intensity increased with colony size. Experimental removal of male swallows during the early nestling period reduced the nest guarding intensity and increased frequency of visits from unmated males in colonies, but not among solitarily breeding swallows. Colonial nests from which the male was removed suffered from infanticide more often than solitary nests, and nests where infanticide was recorded were guarded significantly less intensely than other nests before the infanticidal incidents.

## Introduction

Unmated males are relatively frequent in many monogamously breeding birds and make up a large part of the so-called floating population (e.g. Crook and Shields 1985). The reproductive options of such males are either to attempt to attract a mate or to engage in alternative reproductive strategies without a pair-bond. Mortality rates are high among many passerine species, so the option of postponing breeding until the following year is not really available. Extra-pair copulations are frequent in many bird species (Ford 1983; McKinney et al. 1984; Birkhead et al. 1987), and one would suppose that unmated males especially should engage in such behaviour. However, experienced mated breeders practice extra-pair copulations more often than young unmated males. Experienced males start to breed early and thus have finished mate guarding while neighbouring females of pairs in an earlier breeding stage are still fertilizable (references as above).

In addition, it has recently been realized that unmated males may commit infanticide and thus break up already established pair-bonds (e.g. Hausfater and Hrdy 1984; Crook and Shields 1985). If the breeding season is relatively long, infanticide could lead to a new breeding attempt involving the unmated male. The female would not generally benefit in such a situation unless she mated with a male apparently of a better quality than her previous mate. The superior quality of the unmated male could be revealed by his ability to practice infanticide and by the inability of the male mate to prevent the killing of his own young. Alternatively, infanticidal males may strike opportunistically or take advantage of the resident males' busy breeding schedule and sneak in to kill the young. This explanation, however, does not explain why females suffering from infanticide mate with the infanticidal male rather than disperse and mate elsewhere. Sexually selected infanticide has been reported in a number of polygynous mammals (review in Hausfater and Hrdy 1984), but only in a few bird species (Crook and Shields 1985;

Freed 1986; Goldstein et al. 1986). Although sexually selected infanticide has not been reported in other bird species (Mock 1984), it could have gone unnoticed in many cases (Crook and Shields 1985), being confused with nest predation.

In this paper I examine the causes and consequences of infanticide on the basis of work on the European swallow *Hirundo rustica rustica*, which is a monogamous species living in single pairs or in colonies (Møller 1987c). Furthermore, I describe anti-infanticidal strategies, and finally, I report an experiment on the effect on infanticide of the detention of mated males.

## Methods

### *Study area*

The study took place at Kraghede (57°12′N, 10°00′E), Denmark, in a 15 km$^2$ study area. A detailed description of the study area is given in Møller (1987c).

### *Observational procedure*

Swallows were caught upon arrival in spring during 1983–1986 and given individual combinations of colour-rings and/or dyes on their belly feathers. More than 90% of all adults were thus colour-ringed. The behaviour of individuals was recorded during (sunrise to 1200 h) 2-h morning observations throughout the breeding season (May to early September). More pairs were watched simultaneously in the colonies. All males established nesting territories, and I attempted to record the activities of unmated males in particular. Visits at nests by unmated males were recorded in 1985 in relation to stage in the nesting cycle of visited nests. Extra-pair copulations and extra-pair copulation attempts (see Møller 1985 for a detailed description) were recorded 1983–1985. Nest guarding, which was recorded during the 1985 breeding season, was defined as the percentage of observations every second minute during daily observations of a nest owner being within 2 m of its nest. Mean nest guarding intensity was then calculated using the values for the first 5 days of the nestling period. Nest guarding was split up into (1) total nest guarding (at least one owner near the nest), (2) total male guarding (time spent by male owner near the nest), (3) total female guarding (time spent by female owner near the nest), and (4) male and female guarding together (both male and female owner simultaneously near the nest).

### *Experimental procedure*

During the 1986 breeding season I transported experimental males (10 colonial, 5 solitary) away from their nests after capture late at night (2400–0200) on a randomly chosen day during the first 5 days of the nestling period. Experimental males were released around 0800 h and later returned to their nests during the capture day. Control males were matched with experimentals in relation to start of egg laying (colonial controls: $53\pm5$ (mean$\pm$SD; day 1 = 1 May), colonial experimentals: $53\pm5$, *t*-test, NS; solitary controls: $46\pm9$, solitary experimentals: $45\pm12$, *t*-test, NS). Both control and experimental males were from the same colony in the colonial experiment. Experimental and control status was assigned randomly to males. During removal days I recorded the activities at experimental and control nests during a 2-h morning observation period: visits by unmated males, infanticide (removal of nestlings by unmated males), and nest guarding intensity as described above. During the 1987 breeding season I made similar experiments on 5 control and 5 experimental solitary pairs. Start of egg laying was similar in these two groups (control: $43\pm9$, experimental: $44\pm8$, *t*-test, NS).

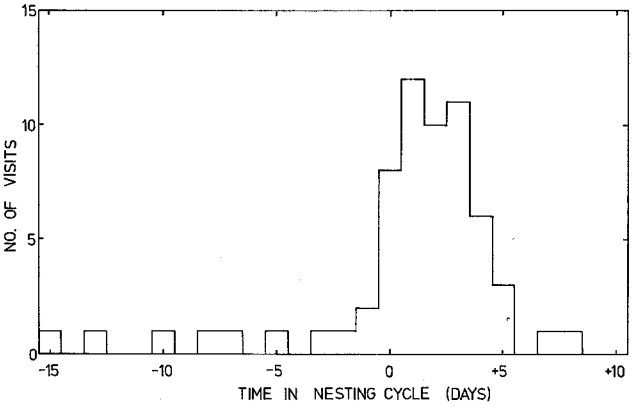


**Fig. 1.** Visits by unmated male swallows at neighbouring nests in relation to time in nesting cycle (day 0 is the first day in the nestling period) during 1985

### *Statistical procedure*

I used non-parametric and parametric statistical tests in accordance with Siegel (1956) and Sokal and Rohlf (1981). All tests are two-tailed unless otherwise stated. Data are given as mean$\pm$SD.

## Results

### *Infanticidal behaviour*

Unmated colonial male swallows visited neighbouring territories, and such visits were particularly frequent during the first days of the nestling period (Fig. 1). Visits were not directed at any particular nests, but unmated males usually tried a number of nests (range 0–5, mean $2.1\pm0.7$ nests, $N=10$ males). In some cases, visiting gradually became concentrated on specific nests where live nestlings were removed by the unmated male. I have directly seen infanticide taking place at three nests where three different unmated males removed all nestlings within a single hour by visiting the nest when it was unattended, picking up a nestling, flying away and dropping it on the ground. Two other cases were reported by farmers who saw two adult colour-ringed swallow males remove live nestlings from a nest during the early nestling period. Finally, I have 9 cases where all nestlings during the first days of their lives disappeared from one day to another probably as a result of infanticidal activities. All these nests were frequently

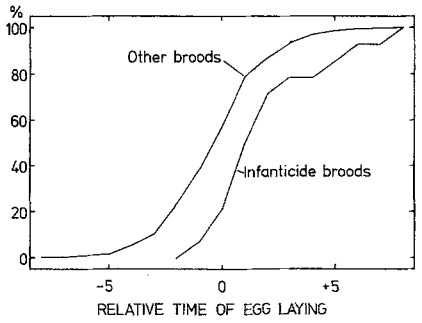


**Fig. 2.** Cumulative time of start of egg laying for infanticide ($N=14$) and other swallow clutches ($N=462$). The *time scale* is in 5-day periods where 0 is the period of maximum laying for each of the years 1978–1986

visited (more than 5 visits per hour) by unmated males during preceding observation periods whereas none of the 299 nests without disappearing nestlings had such a high visit frequency ($G_1^2=81.54$, $P<0.001$). Nestlings disappeared on days 1 to 4 ($2.3\pm1.0$, $N=14$), of their lives.

In the 14 cases reported here, the male swallow of the pair disappeared in 11 cases before infanticide took place (probably died, as was in fact known in 4 cases), and the unmated male which visited the nest and apparently practised infanticide later mated with the widowed female. In the other three cases, the female was still mated when the putative infanticide occurred, but subsequently mated with the killer of her previous brood. Renesting took place in 12 cases, and all these resulted in fledged swallows.

The start of egg laying in the nests that were subjected to infanticide was significantly later than in other swallow nests (infanticide: $58\pm11$, $N=14$, others: $52\pm21$, $N=462$, $t_{474}=2.00$, $P<0.05$). The relatively late breeding start of infanticide victims (Fig. 2) shows that such swallows are generally young first-time breeders which start to lay relatively late following a late arrival.

Males should only attempt to practice infanticide if female victims can renest soon afterwards (Rohwer 1986). Infanticide is thus only predicted to occur in first broods. Infanticide took place in 14 of 298 first broods, but never in 179 second broods, differing significantly from numbers expected according to the number of broods (first broods: 8.74, second broods: 5.26, $G_1^2=13.19$, $P<0.001$).

Infanticide was a major cause of mortality among nestling swallows in my study area. Nearly one-third of the nestling mortality recorded could be attributed to infanticide (Table 1). Other major causes of death were starvation and infection by the haematophagous mite *Ornithonyssus bursa*, whereas death caused by predation was not recorded during the years 1982–1986.

**Table 1.** Mortality of 131 nestlings in 308 swallow broods from 1982–1986

| Cause of death | % of deaths |
|---|---|
| Infanticide | 32.1 |
| Starvation | 29.0 |
| Mite infection | 13.7 |
| Female dead | 6.9 |
| Nest fall | 6.1 |
| Unknown | 12.2 |

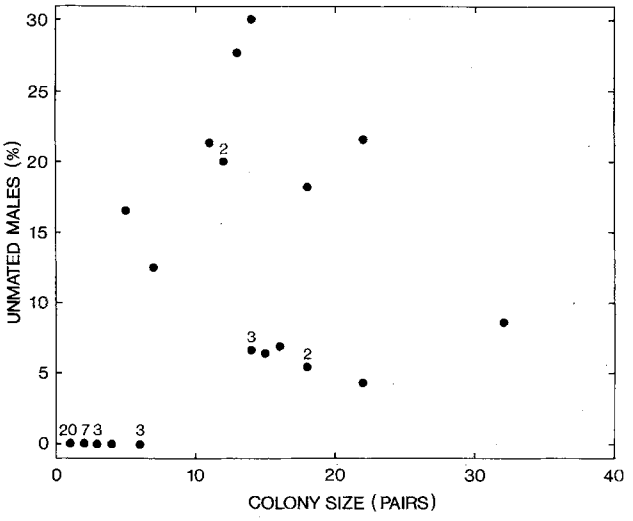


**Fig. 3.** The relative frequency of unmated males (%) in relation to the size of swallow colonies. *Numbers* indicate number of colonies

Infanticidal activities involved a relatively large fraction of unmated males (33%, $N=42$). Only a small fraction of all nests suffered from infanticide (2.9%, $N=476$).

### *Infanticide and coloniality*

The probability that at least one widowed swallow, and thus a potential infanticide victim, is present should be greater in a colony since colonies are made up of many pairs. Unmated male swallows for this reason alone should concentrate in large colonies. If unmated males were distributed in an ideal free fashion they should make up a similar fraction in all colonies irrespective of size, i.e. the fraction of unmated males should not be significantly related to colony size. The fraction of unmated males in fact increased significantly with colony size (Fig. 3; $r_S=0.70$, $t_{50}=7.0$, $P<0.001$).

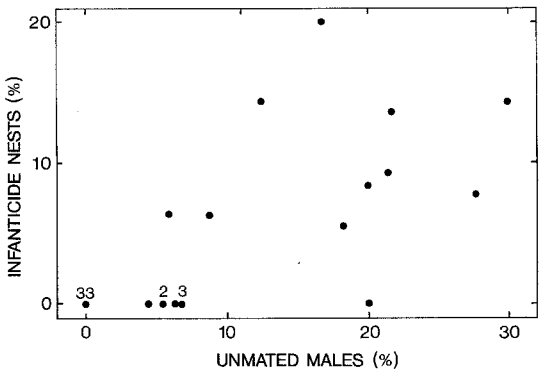


**Fig. 4.** The relative frequency of infanticide nests (%) in relation to the relative frequency of unmated male swallows (%). *Numbers* indicate number of colonies

The fraction of nests suffering from infanticide should increase with the fraction of unmated males, and with increasing colony size per se if some other property of colony size was responsible for the relationship. The relative frequency of infanticide nests increased significantly both in relation to colony size ($r=0.40$, $t_{50}=3.1$, $P<0.01$) and the fraction of unmated males ($r=0.78$, $t_{50}=8.9$, $P<0.001$; Fig. 4). A partial correlation analysis revealed that only the fraction of unmated males was important ($r_{partial}=0.74$, $t_{50}=7.9$, $P<0.001$) whereas the relation to colony size was not significant ($r_{partial}=-0.16$, $t_{50}=1.1$, NS). The infanticide risk per nest increased significantly with colony size ($r_S=0.53$, $t_{50}=4.40$, $P<0.001$).

*Extra-pair copulations as anti-infanticidal behaviour*

Infanticide is apparently a major cause of death among nestlings of colonial swallows, and therefore there should be strong selection for any activity minimizing this loss.

Extra-pair copulations are relatively frequent in swallow colonies, making up 8% of all copulations (Møller 1987b), and by engaging in such extra-marital copulations females may confuse paternity and thus reduce the infanticidal incentive of males (Altmann et al. 1978; Hrdy 1981; Crook and Shields 1985). I recorded extra-pair copulation attempts. Female swallows were able to accept these attempts by staying put or to reject them by behaving aggressively towards importunate males. None of 12 attempts by unmated males was successful (cloacal contact) whereas 18 out of 64 attempts by mated males led to successful extra-pair copulations. This difference is statistically significant ($G_1^2=7.15$, $P<0.01$), but in the direction opposite to that predicted from the anti-infanticide hypothesis. Neighbour males are more successful than others in achieving extra-pair copulations (Møller 1985). The relation between extra-pair copulation success and male mating status was not caused by unmated males having older and more experienced neighbours than mated males (Mann-Whitney *U*-test, NS). All males attempted extra-pair copulations at the same time in the nesting cycle of neighbouring females (Mann-Whitney *U*-test, NS), and extra-marital copulation success was therefore not related to differences in timing of attempts.

*Nest guarding as anti-infanticidal behaviour*

Swallows have small breeding territories of a few square metres. One would expect infanticide to be impossible in the presence of at least one nest owner within the territory. The probability of attack on an approaching unmated male was related to the distance between a nest owner within the territory and an intruder, and intruders within a distance of 2 m were always attacked ($G_4^2=63.51$, $P<0.001$). I thus considered a nest to be guarded if a nest owner was present within a distance of 2 m.

Nest guarding at 20 randomly chosen nests during a randomly chosen day in the nestling period in the morning (between sunrise and 0800 h), around noon (1100–1300) and in the evening (1800 to sunset) was studied in order to check for temporal consistency in nest guarding intensity. Extra-pair copulations are known usually to take place in the morning, probably because fertilization probability appears maximal at that time (Møller 1987b), and nest guarding intensity therefore may vary relative to other behavioural options. Nest guarding intensity, however, was very consistent within pairs in the course of the day (comparison of guarding intensity in the morning, around noon and in the evening: total guarding: $W=0.84$, $\chi_{19}^2=47.7$, $P<0.001$; male guarding: $W=0.78$, $\chi_{19}^2=44.6$, $P<0.001$; female guarding: $W=0.82$, $\chi_{19}^2=46.6$, $P<0.001$; male and female guarding together: $W=0.70$, $\chi_{19}^2=39.6$, $P<0.01$). Morning observations can thus be considered representative of the intensity of nest guarding during the entire day.

If efficient nest guarding prevents infanticide, one would predict than infanticide nests were guarded less often that nests without infanticide. This was also found to be the case (infanticide nest: $44.7\pm12.7\%$, $N=3$, other nests: $81.4\pm9.5\%$, $N=32$, $t_{33}=4.9$, $P<0.001$).

Since unmated male swallows tend to concentrate in colonies, nest guarding during the first 5 days of the nestling period should be more intense in colonially compared with solitarily breeding

**Table 2.** Swallow nest guarding intensity (% time) during days 1–5 of the nestling period in relation to social dispersion

| Nest guarding variable | Nest guarding intensity (% time) (mean ± SD) | | $t_{36}$ | $P$ |
|---|---|---|---|---|
| | Colonial $N=32$ | Solitary $N=6$ | | |
| Total guarding | 81.4 ± 9.5 | 67.8 ± 9.1 | 3.33 | <0.01 |
| Male guarding | 22.0 ± 13.9 | 18.9 ± 13.5 | 0.52 | NS |
| Female guarding | 73.2 ± 9.1 | 58.2 ± 10.9 | 3.16 | <0.01 |
| Male and female guarding together | 13.8 ± 13.0 | 7.8 ± 10.6 | 1.23 | NS |

**Table 3.** Correlations between swallow nest guarding intensity (% time) during days 1–5 of the nestling period and colony size and relative frequency of unmated males, respectively. $N=10$ colonies

| Nest guarding variable | Colony size | | Unmated males | |
|---|---|---|---|---|
| | $r$ | $r_{partial}$ | $r$ | $r_{partial}$ |
| Total guarding | 0.73* | 0.17 | 0.86** | 0.68* |
| Male guarding | 0.55 | −0.25 | 0.82** | 0.75* |
| Female guarding | 0.70* | 0.05 | 0.88*** | 0.75* |
| Male and female guarding together | 0.57 | −0.38 | 0.88*** | 0.84** |

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

swallows. Total guarding and female guarding were also found to be more intense at colonial compared with solitary nests (Table 2). Male guarding and male and female guarding together also tended to be more intense in the colonial breeding situation, although not significantly so.

If the fraction of unmated males increased with colony size, as suggested by the data shown in Fig. 3, one would predict that nest guarding intensity would increase with colony size. This relation should follow from the increasing number of unmated males rather than from colony size per se. Nest guarding intensity increased with colony size and with the fraction of unmated males (Table 3), but when partial correlations were calculated and the effect of colony size was separated from the effect of unmated males, it became clear that the fraction of unmated males was the single important factor (Table 3).

### *A detention experiment*

Data from the observational study suggested that infanticide was practised at infrequently guarded nests by unmated male swallows, especially in colonies where such males were abundant. In order to test these ideas experimentally, I detained males temporarily both in colonies and among solitarily nesting pairs to reduce nest guarding intensity. Since unmated males primarily concentrated in colonies (Fig. 3), I predicted that such males would visit and practice infanticide at experimental nests in colonies, but not at solitary experimental nests.

**Table 4.** Nest guarding intensity (% time) in experimental (male detained) and control swallow pairs

| Experimental status | Social dispersion | Total nest guarding intensity (% time) (mean ± SD) | $N$ | $U$ | $P$ |
|---|---|---|---|---|---|
| Experimental | Colonial | 69.2 ± 19.6 | 10 | | |
| | | | | 22.5 | 0.018 |
| Control Experimental | Colonial | 85.6 ± 12.5 | 10 | | |
| | Solitary | 50.0 ± 7.5 | 5 | | |
| | | | | 0 | 0.0038 |
| Control | Solitary | 77.2 ± 13.0 | 5 | | |

Detention of males for a single morning during the first 5 days of the nestling period caused a decrease in total nest guarding intensity. Removal of the male reduced nest guarding intensity both among colonially and solitarily nesting swallows (Table 4).

Unmated males visited all 10 experimental colonial nests whereas none of the 10 experimental solitary nests were visited during the observations (Fisher exact one-tailed test, $P<0.001$). Similarly, all experimental colonial, but none of the control colonial nests, were visited by unmated males (Fisher exact one-tailed test, $P=3\times10^{-6}$).

Nestlings were removed by unmated males from 4 of 10 experimental colonial nests (1, 1, 1, and 3 nestlings) but from none of the control nests (Fisher exact one-tailed test, $P=0.04$). Nestlings were not removed from solitary nests, differing significantly from experimental colonial nests (Fisher exact one-tailed test, $P=0.04$). Infanticide colonial experimental nests were guarded less intensely than other colonial experimental nests (infanticide nests: 51.3 ± 17.2%, others: 81.2 ± 9.3%, $U=0.5$, $P<0.01$).

## Discussion

Infanticide is apparently a common alternative reproductive strategy among unmated male swallows of the North American *erythrogaster* and of the nominate subspecies (Crook and Shields 1985; this study). A total of 14 cases of observed or circumstantially evidenced infanticide was recorded in my study and 8 cases by Crook and Shields (1985).

Predation was absent from the swallow colonies because all nests were inaccessible to potential predators like cats, and nearly all within buildings which prevented predation by corvids. Starvation does not explain brood mortality in colonies, because entire broods disappeared when nestlings were aged 1–4 days. Starvation did, however, take place when nestlings were 7 days or older. Nestlings that had died from starvation were left in or below the nests.

Infanticide is a cost of coloniality and is higher for individual swallows breeding in large rather than small colonies. The risk of infanticide per capita increased with colony size. Alternatively, solitary pairs may be inherently difficult for other swallows to detect and thus suffer lower risks of infanticidal than colonial nesters. This is highly unlikely because unmated males can easily cover the relatively small study area and because solitary nests regularly had visits by strange males (Møller 1987c). Female swallows could minimize the risk of infanticide either by breeding solitarily or by adopting anti-infanticide behavioural strategies. The cost of infanticide for the female may, however, be balanced by other benefits of coloniality (Møller 1987c). Unmated male swallows did not settle in an ideal free fashion, but tended to aggregate in larger colonies. Unmated males benefited from settling in colonies because of the larger number of opportunities to practise infanticide and gain access to widowed females.

Female promiscuous behaviour is a potential anti-infanticide strategy because the certainty of paternity will then be obscured (Altmann et al. 1978; Hrdy 1981; Crook and Shields 1985). Even though female swallows in general and infanticide victims in particular had the opportunity to engage in extra-marital copulations with unmated males, females only accepted extra-pair copulation attempt from older mated males. Extra-pair copulations are not accepted by females as a component of an anti-infanticide strategy. The fact that unmated male swallows were unsuccessful in obtaining reproductive success by getting a mate or by means of extra-pair copulations may make infanticidal takeover of a female the only strategy left. This strategy will thus also pay such males relatively more than any other strategy.

High nest guarding intensity of nests by a pair seems likely to play a role in reducing infanticide. Unmated males were frequent in colonies, and presumably in order to defend the nest against their infanticidal propensities, the time spent guarding nests during the first days of the nestling period was higher in colonies, and more so in large compared with small colonies. This activity probably competes with other activities like foraging, feeding of nestlings, and extra-pair copulation behaviour. If infanticide takes place at nests with low guarding intensity, there may be selection for increasing the intensity of nest guarding as much as possible. Therefore, division of the guarding activity between pair members will be important for maximising its efficiency. While female nest guarding increased by 15% from solitary to colonial nests, time spent guarding together with male mates increased only by 6% (Table 2), suggesting that guarding was intensified by one of the sexes rather than by a higher frequency of guarding by the pair members. Overall, colonial breeding will have the cost of nest guarding during the critical first days of the nestling period.

Experimental detention of male swallows during the first days of the nestling period caused a decrease in total nest guarding intensity. The attention of unmated males was directed towards experimental colonial, but not towards experimental solitary nests. Subsequently, infanticide was only recorded in experimental colonial nests, and only in those nests where the experimentally 'widowed' female failed to compensate for the loss of nest guarding by the mate. The results of these experiments thus support the observations and confirm that unmated males preferentially visit unguarded nests in colonies and attempt to practice infanticide if given a chance. Thus, the risks of infanticide inherent in colonial life are greater for certain females than for others, as a result of their different capability of defending their nests. Experimental removal of males in Palestine sunbirds *Nectarinia osea* similarly led to infanticide (Goldstein et al. 1986).

Sexually selected infanticide has previously been reported in swallows, purple martins *Progne subis*, cliff swallows *Hirundo pyrrhonota*, house wrens *Troglodytes aedon*, and Palestine sunbirds *Nectarinia osea* (Crook and Shields 1985; Allen and Nice 1952; Emlen 1952; Freed 1986; Goldstein et al. 1986), but is likely to occur also in other species. The most important factors favouring its evolution are (1) colonial breeding which provides more opportunities for unmated males to locate inadequately guarded nests (see also Crook and Shields 1985), (2) asynchronous breeding allowing successful breeding following an initial nest failure (caused by infanticide), (3) a long breeding season with more than one brood per pair per season (for the reasons mentioned in (2), (4) a skewed sex ratio, (5) low relatedness between colony members, i.e. absence of kin selection (Crook and Shields

1985), and (6) high annual adult mortality rates which will discourage postponement of breeding to a following year. Potential infanticide candidates in the European avifauna include house martin *Delichon urbica*, sand martin *Riparia riparia*, fieldfare *Turdus pilarus*, house sparrow *Passer domesticus*, tree sparrow *Passer montanus*, and perhaps jackdaw *Corvus monedula*.

My experiment revealed that male participation in nest guarding is important because it will increase the guarding intensity to a level which will prevent infanticide. The importance of male participation in the rearing of offspring is thus enhanced by the reproductive tactics of other males. Nest guarding in the swallow is also important in order to prevent intra-specific nest parasitism (Møller 1987a), and one might speculate that the increased paternal share of the breeding activities may reduce the male's opportunity to seek extra-pair copulations. In general, the outcome of sexual selection and the variance in male life time reproductive success will be determined in part by the reproductive tactics of conspecifics.

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