territorial. This trend was reversed when the trout farms were reopened one year later. A flexible social system may be an adaptation to food resources that fluctuate from year to year. Magpies seem to respond to an abundance of food resources by increasing densities, clustering nests about the locations of rich resource patches, and abandoning territorial defense. When disturbance to nests is low this can approach coloniality. In years when resources become unavailable or are found in low levels, magpies respond by spacing nests farther apart suggesting a switch to territoriality.

In years when nesting density decreased and nests were uniformly spaced, the mean number of young fledged per nest tended to increase (Fig. 2). There are several factors such as predation or climate that influence reproductive success that we were unable to measure for or control. Without doing so, we would be unable to conclude that reproductive success was or was not density dependent. Reproductive success does appear to be density dependent for this population of magpies and is also perhaps influenced by nest dispersion. Thus, the interaction between density, nest dispersion and reproductive success should be examined more thoroughly by future studies.

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INFANTICIDE IN FEMALE TREE SWALLOWS: A ROLE FOR SEXUAL SELECTION[1]

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Key words: Sexually selected infanticide; replacement female; Tachycineta bicolor; *Tree Swallows.*

The recognition that infanticide, the killing of conspecific young, can hasten or even create a breeding opportunity for the infanticidal adult, has elevated the behavior from pathological to sexually selected. The apparent rarity of this behavior in the avian world (Rohwer 1986) has been attributed to the prevalence of monogamy among bird species and therefore a limited substrate upon which sexual selection could act (Mock 1984). However, even in monogamous species, competition for breeding opportunities may be intense due to factors such as biased sex ratios or limited nesting sites. Hence, sexually selected infanticide may be expected and indeed has been shown to occur in monogamous bird species (e.g., Crook and Shields 1985, Goldstein et al. 1986, Freed 1986, Robertson and Stutchbury 1988, Møller 1988, Veiga 1990).

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One such monogamous species in which male sexually selected infanticide occurs is the Tree Swallow, *Tachycineta bicolor.* Robertson and Stutchbury's (1988) study suggested a short breeding season and a short life expectancy (Butler 1988) as factors creating intense pressure to breed in any given season (Studd and Robertson 1985). Moreover, they observed that the limitation of breeding opportunities imposed by secondary cavity nesting status (Holroyd 1975) and the floating populations of both sexes that result (Stutchbury and Robertson 1985) combine to favor the evolution of an infanticidal tactic. Specifically, any male that is able to evict or replace a resident at a nest site might expedite his own breeding by destroying the nest contents, whether they be eggs or nestlings. There is little reason to expect restraint on the part of a replacing male Tree Swallow since relatedness is low in tree swallow populations (De Steven 1978, Robertson and Stutchbury 1988) and a victimized female who deserts will likely be quickly replaced from the ranks of the reproductively mature floaters.

Because female Tree Swallows face, to some degree, similar pressures and limitations as compared with males, we predicted that Tree Swallows would join tropical House Wrens, *Troglodytes aedon* (Freed 1986) and House Sparrows, *Passer domesticus* (Veiga 1990) in being one of a few species in which both sexes are known to commit infanticide. While anecdotal accounts (Shelley 1934, Robertson and Stutchbury 1988) reveal that female infanticide is by no means unknown in this species, we attempted to supplement these accounts with an experimental approach. We report here the results of a female removal study in which the responses of replacement female tree swallows to eggs and nestlings were documented.

STUDY AREA AND METHODS

This study was conducted during May and June of 1990 at the Queen's University Biological Station located on Lake Opinicon about 50 km NE of Kingston, Ontario. Established, on the lake, are two grid-like arrangements of 25 nest boxes, sparse and dense, in which the nearest neighbor distance between boxes within rows is 40 and 20 m respectively. The distance between rows is 20 and 10 m but because the rows are offset with respect to one another, the nearest neighbor distance between rows is on the diagonal and is 28 and 14 m respectively. Annual occupancy is 100% and there is a floating population of males and females (Stutchbury and Robertson 1985).

We removed, by trapping in the box (Stutchbury and Robertson 1986), four females (30 May–1 June) during late incubation and four (three on 6–7 June, one on 20 June) during the first two to three days of the nestling period. We checked the nests of incubation stage widowers (ISW) every day but no formal behavioral observations were made since, to our knowledge, past studies have never revealed an instance of tree swallows, of either sex, removing intact eggs. The nests of nestling stage widowers (NSW) were watched every day for at least two hours unless or until the nestlings died from starvation or infanticide, or the resident male appeared to have deserted, or inclement weather drove the birds from the study area. One resident male was able to keep some nestlings alive for eight days and was patently aggressive to all potential replacements so we reduced watches at this box to one hour a day after four days.

RESULTS

All four ISW obtained replacement females within 36 hours of their original female being removed (maximum possible time until replacement occurred $\bar{x}$ = 31.5 h, SD = 5.2). All females re-lined the previous resident's nest cup within 24 hours of arriving at the nest. In two cases this re-lining entailed completely burying the former female's eggs with about 1 cm of grass or aquatic weed. In contrast, minimal re-lining at the two other nests resulted in later mixing of the replacement female's clutch with eggs from the previous female's clutch. All of these female replacements commenced laying eggs in the nest of the resident male within six days of their arrival (minimum possible time to first egg $\bar{x}$ = 4.8 days, SD = 0.96). We saw replacement females copulate with the resident male in two cases.

Of the four NSW, only two obtained replacements, both during the period when their nestlings were still alive. Of these two replacement females one appeared indifferent to the live young, the other committed infanticide. The non-infanticidal female replacement, a sub-adult, arrived within 30 min of the resident female being removed on nestling Day 2. She entered the box on many occasions for minutes at a time, but periodic checks revealed no detectable injuries to the nestlings. The male was at first noticeably aggressive to the female, frequently chasing her and guarding the nest hole, but seemed to accept the female by the time of the nestlings' death by starvation, despite the male's feeding attempts, on nestling Day 3. Exposure was also a possible cause of death as nestlings are usually brooded by the female for 10–11 days and males have no brood patch and are not known to brood (pers. obs.). Examination of the dead nestlings did not reveal any injuries. All but one dead nestling subsequently disappeared from the nest, presumably having been removed by one of the pair. The replacement female at this nest laid her first egg in the re-lined nest on 11 June, five days after her arrival.

At the other nest to receive a replacement, the infanticidal female, a subadult, was first sighted approximately 48 hr after the resident female's removal, late in the afternoon of 9 June. Of eight nestlings that had been alive and unharmed that morning two were now dead, apparently from starvation or exposure. However, of the six remaining nestlings, five were multiply pecked and bleeding and had deep contusions on their heads and bodies. We refer to these as "injured." The following morning the nest contained the two "starved" dead nestlings, four "injured" dead nestlings and one "injured" live nestling. One of the nestlings that had been alive the previous day had been removed, presumably by one of the pair. Two hours after the nest check we saw the female remove a dead "injured" nestling. Because we could not be certain that the female, and not starvation, had caused the death of four of the five "injured" nestlings we removed the one "injured" nestling that remained alive and replaced it with a healthy nestling from a neighboring nest. We refer to this as the "foster" nestling. The replacement female next removed one of the "starved" nestlings and a dead "injured" nestling in quick succession. A nest check revealed that the "foster" nestling had by then three head contusions and a peck mark after being in the nest for about an hour. Twenty-five minutes later this nestling was removed by the female and dropped in the water. It is not clear whether the "foster" nestling was alive when it was removed as we were unable to recover it. Regardless, we can be sure that the female alone was responsible for its death since it was healthy when it was introduced to the nest and the male did not enter the nest in the intervening time. The female removed one more nestling during the watch. By the following morning all the nestlings had been removed. The female laid her first egg in the re-lined nest six days after her arrival at the nest.

The remaining two NSW males, who did not receive replacements, both deserted within 24 hr of the nestlings' deaths (occurring one and eight days after the respective females' removal). One of these males had no intrusion events (birds flying within 5 m of the nest box, hovering near the box or perching) probably due to the inclemency of the weather, the lateness of the season (post 20 June), and the short time (one day) between his female's removal and his own desertion. The other male had multiple intrusion events during the eight days prior to his desertion and, like the two NSW males who did eventually receive replacement females, this male initially adopted a defensive posture toward intruders following the removal of the resident female (unpub. data). These three males tended to respond to intruders by either chasing the offending bird or guarding the entrance to the box even when the intruder's brown plumage clearly identified it as a female and thus a potential mate. At the three NSW nests experiencing intrusion events, the complete cessation of aggression toward intruders by the resident males coincided with the deaths, by starvation or exposure, of some or all nestlings in the respective nests.

DISCUSSION

The variability in the response of replacing females in our study toward the offspring of the NSW, as compared to that of replacing males (Robertson and Stutchbury 1988), might be expected considering the perspectives of the replacing individuals. Males face the potential loss of a breeding opportunity if they allow the widow to raise even a partial brood. Thus there is intense selective pressure to be infanticidal. Females may face only a delay of their breeding opportunity by allowing the widower to blunder toward the fruitless conclusion of his parenting effort as opposed to seizing the first opportunity to kill the nestlings. The gains in time engendered by female infanticide might often be outweighed by the potential costs, such as those involved in combatting a militantly defensive male, resulting in the evolution of a conditional infanticidal tactic.

The fact that two of the four NSW failed to receive replacement females may be because one male defended his nest against intruders until all the nestlings died on 15 June while the other male was not widowed until 20 June and was not visited by any conspecifics after this time. It is rare for females to initiate breeding attempts this late in June (Robertson and Stutchbury 1988).

Aggression toward intruders may reflect an attempt on the part of widowers to defend against potential usurpations of their nest by intruders until it becomes obvious that their mate is not returning. After this time they may defend the nest against intruders unless or until some or all of its contents (eggs or nestlings) are dying, have died, or been killed. At this point they may abandon care of their offspring, defense or feeding, in favor of an expeditious re-mating with any willing attendant female. While we have no data on the response of ISW to intruders it is worth noting that all of the ISW received replacement females in substantially less time than the NSW. This is not likely to be a function of relatively more intrusion events earlier in the season, at least by subadult females (Stutchbury and Robertson 1987), but it could be that as the season wears on a larger proportion of the intruder females are merely exploring breeding possibilities for the next season (Stutchbury and Robertson 1987). Alternatively, the difference in receptivity to replacements in the widower groups may correspond to the difference in the probability of survival of the nest contents as time without female care increases. While data on Passerines are extremely scarce, available information from other studies on the effect of temperature on embryos (reviewed in Webb 1987) suggests that relatively short periods of exposure, even a matter of hours, to suboptimal temperatures can cause mortality and that the percentage mortality increases with the age of the embryo. In contrast, Tree Swallow nestlings may last days without brooding (this study). As a consequence, widowers left with eggs might more rapidly reach the situation where they have nothing to lose by abandoning hope of their mate's return and mating with any willing female.

The absence of a brood patch in the male, and thus his inability to incubate the eggs, may be exactly why replacement females do not destroy the eggs laid by the former resident female. The extant eggs cannot be directly invested in by the male to the detriment of any clutch yet to be laid by the replacement female, nor is it likely that their destruction by the replacement female would hasten the onset of mating with the male. In the absence of any obvious selective advantage to disposing of the eggs the default behavior would appear to be indifference. If the re-lining of the nest cup serves to isolate the former resident's eggs from the replacement's clutch eliminating the possibility of accidental incubation, hatch, and misdirected nurture, then it might be argued that the eggs elicit a response rather than indifference. However, even in those nests in which re-lining was minimal and eggs from both clutches essentially mixed freely we observed no cases of the former female's eggs hatching. From records of natural female turnovers this season, we suspect that re-lining of the nest, ranging from token additions of material to complete excavations of the nest cup, is a general response of replacement females to their new nests, regardless of the contents, and should not be construed as infanticide.

We suggest that infanticide committed by female Tree Swallows might hasten the procurement of an unencumbered nest site, that is, a nest site not burdened by another female's nestlings. It is important to note the differing viewpoints of the sexes with respect to the significance of an unencumbered nest site. For a male Tree Swallow reproductive success, however modest, hinges on the opportunity to fertilize a female with such a nest site, either as a member of a pair, or by extra-pair fertilization of an already-paired female (cuckoldry), or both. Since males cannot incubate or brood, the value of a nest site to a male possessing it lies principally in its ability to attract a fertilizable female who will in turn incubate and brood. For female Tree Swallows, however, it is only the degree of, not the opportunity for, reproductive success that is likely to be determined by the presence of a male through his contribution to nestling feeding. Since being fertilized by a male whether floater, already-paired, or mate, is unlikely to be a problem, it is the possession of an unencumbered nest site itself (intraspecific brood parasitism is extremely rare in this population—unpub. data) that is of primary importance in determining whether a female will have the opportunity to reproduce. Since the seasonal reproductive success of a female without such a nest site, or one who waits too long for a nest site, is zero, we suggest that if infanticide committed by female Tree Swallows accelerates the acquisition of a usable nest site, and hence the opportunity to reproduce, then this behavior should be regarded as sexually selected. We recognize and advocate the expansion of the definition of sexual selection that this view requires, from the male-oriented "variance in the opportunity to mate" to the female-inclusive "variance in the opportunity to reproduce." Ultimately, it may be individual factors such as prior breeding experience, the degree of defense of the nest site by the resident male, the life expectancy of the nestlings at the time of the female's arrival or the advancement of the season, which determine for prospective replacement female Tree Swallows whether or not the potential gain in time warrants an infanticidal tactic.

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