

## Short-term and Long-term Consequences of Predator Avoidance by Tree Swallows (*Tachycineta bicolor*)

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In the presence of a potential nest predator, birds commonly respond with distraction displays or alarm calls, mobbing the predator, or avoiding the area entirely (Curio 1976). Model predators have been used to elucidate the adaptive basis of such behaviors and determine the conditions under which birds are willing to defend their nests or expose themselves to predators (references in Knight and Temple 1986, Montgomerie and Weatherhead 1988). Most of these studies, couched in the framework of life history theory, interpret the antipredator behavior of birds as a reaction to the direct threat of injury or death to themselves or to their offspring (e.g. Hoogland and Sherman 1976, Shields 1984, Curio and Regelman 1985, Brown and Hoogland 1986). Increased mortality risk is presumed to be the major fitness cost to birds when a predator is near their nest.

There may be other costs imposed by the presence of a potential predator. Nestling feeding opportunities may be missed when the presence of a predator forces parents to abandon their nests temporarily. Time or energy that could have been used for attracting mates or foraging may be diverted to antipredator behaviors (e.g. Powell 1974, Biermann and Robertson 1983, Conover 1987; cf. Martindale 1982). Predators could indirectly reduce the fitness of nesting birds if the birds' expenditure of extra energy made them more vulnerable to other sources of mortality, or if the disruption of parental care resulted in the production of offspring that were less likely to survive to reproductive age.

Dring and Dring (1984) reported a possible example of a predator indirectly decreasing the fitness of breeding birds. Ring-billed Gulls (*Larus delawarensis*) perching on Tree Swallow (*Tachycineta bicolor*) nest boxes caused the parent swallows to reduce the rate at which they fed their nestlings, which in turn apparently slowed nestling development and prolonged the nestling period by approximately 25% at one nest. Nestling growth rates in Tree Swallows are known to be related to food availability (Quinney et

al. 1986). If the response of birds to a perceived risk of predation extends the period of parental care or elevates foraging costs, and if these effects diminish the probability that parents or their offspring will survive, these frequently neglected costs of avoiding predators could have evolutionary implications.

On Kent Island, New Brunswick, Canada, Tree Swallows nest within a colony of Herring Gulls (*Larus argentatus*). The gulls perch on swallow nest boxes, which they use mostly to monitor their own nearby nests. When the opportunity arises, however, gulls seize and eat adult swallows as they leave the nest boxes or enter them to feed their nestlings (pers. obs.). Swallows respond to gulls perched on their nest boxes by mobbing them or simply staying away from the nests until the gulls leave. We report the results of an experiment to determine whether the avoidance of potential predators near their nests has any short-term effects on the growth rate of nestling Tree Swallows, and whether these effects translate into long-term costs in future reproductive success and survival (cf. De Steven 1980, Nur 1988).

The study area, the Bowdoin Scientific Station, is on Kent Island, an 80-ha island located 9 km south of Grand Manan Island in the Bay of Fundy (44°35'N, 66°46'W). Since 1935, Tree Swallows have nested in artificial nest boxes erected at 30-m intervals in a former hay field in the center of the island (Paynter 1954). At Kent Island Tree Swallows are single-brooded. The colony currently comprises approximately 100 pairs of Tree Swallows (Wheelwright et al. in press). Paynter (1954) described in detail the natural history of Kent Island Tree Swallows and Williams (1988) described their energetics during the breeding season. Almost all breeding females and their nestlings, as well as many males, have been banded with numbered aluminum bands since 1966. Kent Island also supports a large colony of Herring Gulls, which nest in the center of the island at an average density of ca. 6 pairs/ha (cf. Cannell and Maddox 1983). Each breeding season we found 10–20 bands of adult and fledg-

ling swallows in gull castings and observed on several occasions gulls capturing fledgling swallows on the wing.

Every swallow box has some sort of "guard" on top to discourage gulls from perching, but it was difficult to exclude gulls altogether from boxes. In daily scan censuses of 109 active nests during the period 12–21 June 1987, we noted gulls perched on 3 different nest boxes. At these 3 boxes, gulls were present in 23% of the censuses. Gulls were seen on top of at least 10 other nest boxes in 1987. To determine the effect on swallows of gulls perching on their nest boxes, we placed lifelike Herring Gull models (Cabela's Co.) on a group of nest boxes according to the following procedure.

We selected 12 nests with the same hatching date (14 June 1987). Nestlings within a brood were approximately the same age, because Tree Swallow nestlings within a nest generally all hatch within a 1–2 d period at Kent Island (Paynter 1954). Each nest was matched for clutch size as closely as possible with another nest. Within each of the 6 pairs, one nest was randomly assigned as a control, the other as an experimental. Mean ( $\pm 1$  SD) clutch sizes for controls ( $5.8 \pm 1.2$  eggs) and experimentals ( $5.7 \pm 1.2$  eggs) were similar (paired *t*-test,  $P = 0.81$ ). We determined the identity of female parents by capturing them at least twice during incubation and recording their band numbers. There was no significant difference in age between control ( $2.7 \pm 1.2$  yr) and experimental ( $3.2 \pm 0.4$  yr) females (*t*-test,  $P = 0.36$ ). Male swallows share in the feeding of young (Leffelaar and Robertson 1986), but it is often difficult to determine their identity because they do not incubate and hence are not as easily captured as females (De Steven 1980). Therefore, in this study we concentrated on the effect of predation risk on nestling growth, fledging success and survival, and the survival of female parents. Because of Kent Island's isolated location, and the fact that Tree Swallows are highly philopatric and nest almost exclusively in nest boxes on the island (Paynter 1954, Wheelwright et al. in press), we used return rates in the following year to estimate annual survival.

When nestlings were 2 days old, they were weighed to 0.1 g on a portable electronic balance. A gull model was then placed on top of each experimental nest box in the position used normally by perching gulls. Two hours later (a period chosen to approximate the natural occurrence of gulls on affected nest boxes, as noted above), we removed the model and weighed the nestlings again. The same procedure was used for controls except that no gull model was placed on their nest boxes. Experiments at each matched nest pair were staggered by 1-h intervals starting at 0800 daily; thus, we observed each nest for 2 h daily. All nestlings from a pair of nests were weighed within 15 min of each other. At a given nest pair, the experiment began at the same time each day and was repeated for 9

consecutive days. We ended the experiment 11 days after the nestlings hatched because the mass of nestling Tree Swallows begin to plateau shortly thereafter and because we wished to eliminate the risk of premature fledging by handling birds late in the nestling period (Paynter 1954, De Steven 1980). Nestling masses were log-transformed, and the slope of each individual's growth curve was calculated by regressing its mass against its age (for all correlations,  $P < 0.01$  and  $r^2 = 0.95$ – $0.99$ ). The slopes of individual growth curves were then averaged within broods because the brood, rather than individual nestlings, is the appropriate level of analysis, given the likely nonindependence of nestling masses within a brood. Using Statview SE (Abacus Concepts 1988), we compared survival and growth rates of control and experimental broods with standard nonparametric tests and paired *t*-tests.

To determine the effect of gull models on parental behavior, we used 7-power binoculars to observe nests from approx. 30 m away. At 5 nests we recorded feeding visits during 30-min periods immediately before we placed the gull model, and then again for 30 min after placement. At two nests we also counted visits for an additional 30 min after the removal of the model. At one control nest we counted visits over a 30-min period, approached the nest but did not place a gull model on it, and then counted visits for the next 30 min.

When live Herring Gulls perched on top of Tree Swallow nest boxes, the swallows gave alarm calls and frequently dove at the gulls, but we never saw the swallows enter their nest boxes. The swallows showed similar behavior towards the gull model. In the absence of the model, swallows entered their nest boxes to feed young at an average rate of 18.1 trips/30 min ( $\pm 9.7$ ). In the presence of the model their feeding rate dropped to 1.0 trips/30 min ( $\pm 2.0$ ) (paired *t*-test,  $n = 5$  observation periods,  $P < 0.001$ ). Once the gull model was removed, feeding rates returned to normal ( $19.0 \pm 9.9$  visits/30 min,  $n = 2$ ). We attribute the sharp drop in feeding rate mainly to the presence of the gull model rather than to investigator disturbance. Swallows were accustomed to the presence of researchers and being handled by them, and they returned quickly to their nests after being approached. At a control nest, where no gull model was used, the parents made 17 trips in the 30 min before we approached their nest and 9 trips in the next 30 min, an insignificant difference (exact binomial test,  $P = 0.12$ ). Numerous additional observations confirmed that experimental swallows reacted to the model as if it were a real gull, but that control swallows typically behaved normally during the experiments.

The decline in parental feeding frequency during the 2 h when the gull model was present each day resulted in reduced weight gain over that period among experimental nestlings relative to controls (Fig.

1). Controls gained significantly more mass than experimentals on each day of the experiment (paired *t*-test,  $n = 6$  broods,  $P < 0.05$  except when nestlings were 7 days old,  $P = 0.08$ ). The swallows showed no sign of becoming habituated to the model, as evidenced by behavioral observations or nestling weight loss. In fact, daily weight loss among experimental broods in the presence of the model increased significantly as the experiment proceeded (Spearman rank-order correlation,  $r_s = 0.59$ ,  $P < 0.001$ ,  $n = 9$  days; cf. Fig. 1).

By the following day, however, there was no apparent effect of the gull model on nestling mass. Each day at the beginning of the experiment the masses of control and experimental nestlings were not significantly different (Fig. 1; paired *t*-test,  $P > 0.05$  for each day, analyzed at the level of the brood as well as nestlings). Most important, there was no significant difference in mass between controls ( $20.6 \pm 1.8$  g) and experimentals ( $20.9 \pm 1.4$  g) on the ninth and final day of the experiment (paired *t*-test,  $P > 0.20$ ), which suggests that fledging mass was unaffected by the repeated presence of the model predator.

Brood-mean slopes of log-transformed growth curves also did not differ between control and experimental treatments (paired *t*-test,  $P = 0.77$ ). The presence of the gull model did not extend the nestling period: control nestlings fledged on average  $21.8 (\pm 1.3)$  days post-hatch, and experimentals fledged  $21.2 \pm 1.3$  days post-hatch (paired *t*-test,  $P = 0.27$ ). Controls and experimentals did not differ in fledging success, which was 100% for both groups.

Although sample sizes were small, it is clear that the presence of the "predator" did not have a major negative effect on the survival for either female swallows or their offspring. In 1988, 3 of 6 control females and 4 of 6 experimental females were recaptured (Fisher's exact test:  $P \approx 1.0$ ). In the population as a whole, 54 of 107 (50.5%) females returned the following year. Of the 3 control and 4 experimental females that returned in 1988, only 1 (an experimental bird) was resighted in 1989, 2 yr after the experiment. Nestlings also showed no negative long-term effect of the experiment: 1 of 35 controls (2.9%) reappeared in 1988, as compared with 3 of 32 experimentals (9.4%) (Fisher's exact test:  $P = 0.55$ ). In the population as a whole, 13 of 453 (2.9%) banded nestlings returned the following year.

We believe the experiment showed that parent Tree Swallows responded to the perceived threat of predation by Herring Gulls by cutting back the rate at which they fed nestlings to only 5% of their normal feeding rate. During the period when model gulls were perched on their nest boxes, nestling swallows typically went unfed and lost mass. However, the effect was only a short-term one. Twenty-two hours later, the masses of experimental nestlings were indistinguishable from those of control nestlings. Growth rates were similar, as were masses at 10 days

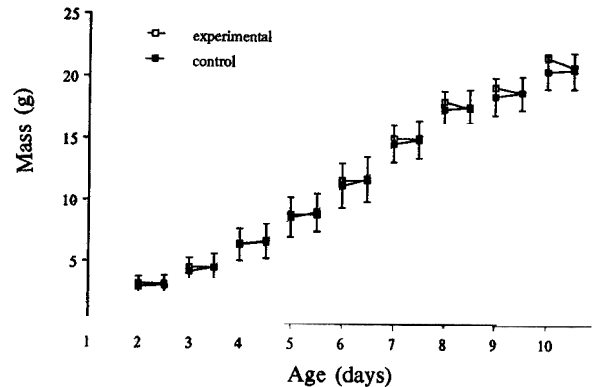


Fig. 1. Nestling age (days) vs. brood mean mass (g) for experimental (open boxes) and control (closed boxes) Tree Swallows on Kent Island. Error bars represent  $\pm 1$  SD. For each day there are two points, the first representing nestling mass at the beginning of the experiment, the second representing nestling mass 2 h later.

of age. The duration of the nestling period and the probability of fledging did not differ between treatments. Moreover, the return rate a year later (a measure of survival rate) of nestlings exposed to predators was equal to that of control nestlings. The same was true for their mothers. Apparently, parents whose nestling feeding schedules were disrupted because they avoided "predators" near their nests were able to compensate either by accelerating nestling feeding rates or by delivering higher-quality food items once the gull model was removed. Harris (1979) studied the costs of intraspecific nest defense in the same population of swallows and found a comparable result: nestlings whose parents had spent extra time and energy in intraspecific aggressive interactions suffered no reduction in fledging success, growth rate, or mass at fledging. Similarly, when Tree Swallow nestlings were deprived of food for 4 h per day during the middle of the nestling period, Wiggins (1990) found no differences between control and experimental nestlings 16 days post-hatch. Although our study showed clear negative effects of avoiding predators over the short-term (2 h), differences in nestling growth rates were erased within a day, and we found no long-term costs.

There are several possible explanations for the lack of any measurable intermediate or long-term effect due to predator-induced reductions in nestling feeding rates. First, despite our efforts to control clutch size, experimental nests averaged 0.5 fewer nestlings per nest than controls. If the effects of decreased nestling weight gain on later growth and survival were subtle, they may have been masked because experimental pairs had slightly fewer offspring to feed. Second, fledging success among experimental and control broods was exceptionally high; 1987, the year the experiment was conducted, was apparently a partic-

ularly favorable year (cf. Paynter 1954). The mean fledging success (fledglings/egg) for Kent Island's Tree Swallow population as a whole, for example, was  $0.84 \pm 0.35$  ( $n = 98$  nests) in 1987 as compared with  $0.65 \pm 0.39$  ( $n = 101$ ) in 1988 and  $0.81 \pm 0.32$  ( $n = 74$ ) in 1989. Perhaps in years of high food abundance, parent swallows—accustomed to unpredictable food availability anyway—can easily compensate for the loss of 2 h of feeding time per day. The “predator” threatened experimental birds for only approx. 15% of nestling feeding time over 9 days; during that time, parents could have been fulfilling their own nutritional needs. Had the experiment been extended an additional 1–2 h each day (Wiggins 1990) or performed at irregular intervals throughout the day as in the natural situation (Dring and Dring 1984), or had it coincided with severe weather or a shortage of insect prey, when metabolic costs would have been raised (Williams 1988), there may have been a noticeable negative effect of the presence of the gull model. Except under extreme conditions, the short-term effects demonstrated here would be unlikely to carry over until the next year (e.g. Alerstam and Högstäd 1984, Ekman and Askenmo 1986), so it is not surprising that we found no long-term cost (but see Nur 1988).

This experiment was designed to evaluate the costs of avoiding a potential predator during the nestling period rather than during the incubation period. Interrupting incubation because of the presence of predators almost certainly would elevate the energetic expense of incubation (e.g. Jones 1989, Williams 1988) or reduce hatching success (Boersma and Wheelwright 1979).

We conclude that the short-term effects of predator-induced disruptions in nestling feeding represent a trivial fitness cost compared with the mortality risks that adults face when they attempt to feed nestlings while a gull perches on their nest. At 1 of 5 nests where parental feeding behavior was observed, one female entered several times under the beak of the gull model. Judging from observations of adult swallow bands in gull castings and the discovery of beheaded birds in boxes, the fitness consequences of “running the gauntlet” could be extreme. The traditional assumption that increased mortality risk is the major cost of exposure to predators (Hoogland and Sherman 1976, Shields 1984, Curio and Regelmann 1985, Brown and Hoogland 1986) is probably justified except under stressful environmental conditions, because the indirect effects on fitness that predators may cause by elevating parental energetic costs or reducing nestling growth rates do not necessarily translate into fitness losses for parents or their offspring.

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