

CAUSES AND CONSEQUENCES OF VARIATION IN PARENTAL DEFENSE BEHAVIOR BY TREE SWALLOWS¹

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Abstract. In a three-year experimental study of parental defense behavior in Tree Swallows (*Tachycineta bicolor*), I presented live ferrets and rat snakes to parents in the vicinity of 113 nests on the 13th and 14th day after chick-hatching. Sex of the defending parent and the identity of the predator being defended against were the most significant determinants of variation in the 13 aspects of parental defense behavior measured. Males defended more aggressively than did females. This may be a correlate of stronger territorial behavior in this sex, rather than a strategic response to differing relatedness to the brood. Ferrets were defended against more strongly than were snakes. This may be a response to greater efficacy of defense behavior against ferrets. Attendance measures of the male and female parent at the nest are highly correlated, whereas intensity measures are much less so. Even those intensity measures that are significantly positively correlated have distributions with many pairs in which one parent does considerable defense and the other does none. I suggest that parents are monitoring each other in the presence of the predator and refraining from defense to get their mates to defend actively. On the basis of observations of defense against many species, I suggest that defense has three functions in Tree Swallows: Intimidation of small nest-site competitors, "moving on," and distraction of larger nest predators. There is evidence that variation in both the costs and benefits of defense are important in affecting its intensity. Despite the large number of potential determinants examined, a large proportion of the variance in parental defense behavior remained unexplained. This large residual variation may be either an adaptation to avoid predator localization of the nest or enhance distraction, or a result of relatively low selective pressures or low frequencies of encounter between predators and swallows.

Key words: *Tree Swallow; Tachycineta bicolor; anti-predator behavior; parental care; life-history evolution.*

INTRODUCTION

Parental care is one of the most obvious aspects of the life histories of most birds, and it is the aspect of avian reproductive effort in which behavior is most intimately involved. The parental care behaviors of altricial birds generally consist of incubating the eggs, feeding the young and protecting the eggs or chicks against predators through some sort of distraction displays or active defense.

Recently, there has been increasing interest in the parental defense behavior of birds. Much of this interest has focused on theoretical predictions of the effects of various potential determinants of variation in defense intensity. The most comprehensive of these has been the model of Redondo (1989), who adapted the general parental care model of Winkler (1987) for the special case of parental defense. Redondo reviewed the literature as it related to his model, and the recent review by Montgomerie and Weatherhead (1988) complements his paper with a wider-rang-

ing non-mathematical review that touches on many general issues as well as contributing original ideas to the field. One of the conclusions that emerges from these recent reviews is that parental defense behavior is extremely variable and can respond to a large number of determinants.

Montgomerie and Weatherhead (1988) also concluded that the costs and benefits of parental defense are poorly understood. This is especially important if defense is to be predicted from life-history models because such models are inappropriate unless variation in the chosen measure of parental defense has benefits (in the form of enhanced offspring production) and costs (in the form of increased costs or risk to the parent) (Winkler and Wilkinson 1988). If these conditions are not met, the models have no basis for optimizing parental defense and predicting its level.

Here I present data germane to these issues from a three-year study of the Tree Swallow (*Tachycineta bicolor*) conducted near Ithaca, New York. I first present results on the importance of various potential determinants of variation in parental defense. Although a few strong deter-

¹ Received 29 July 1991. Accepted 12 February 1992.

minants will emerge, one interesting finding is that most variability in the behavior remains unexplained. I then consider the accumulated evidence on the effectiveness and costliness of parental defense.

METHODS

Observations were made in 1986, 1987 and 1988 on a population of swallows breeding in a grid of 105 nest-boxes. The nest-boxes were erected in 1985 around a series of 41 experimental ponds (0.04 ha each) and a 4.8 ha lake located 10 km north (42°30'N, 76°28'W) of the campus of Cornell University in Ithaca, New York. Each box is within 2 m of water and has its nearest neighboring box 20 m away. In any given year, the majority of Tree Swallow pairs was included in an experiment testing the importance of past investment and expected benefits on parental investment (Winkler 1991). To create differences in past investment and expected benefits, the pairs were assigned to either a control group or one of two experimental groups that had their number of offspring reduced early or late in the nesting cycle. In each year, some pairs were excluded from any of these groups to retain balance among groups for female age, timing of clutch initiation, egg size and clutch size (Winkler 1991). These "non-experimental" pairs were still subjected to the same regimen of regular monitoring, parental capture at the nest and observation of parental defense as were all the pairs in the three groups from the experiment. For this reason, the analyses presented here are based on all of the pairs nesting at the plot in each year, regardless of group membership, and the resulting sample included 28 pairs in 1986, 42 in 1987, and 43 in 1988.

OBSERVATIONS OF PARENTAL DEFENSE

Parental defense behavior was observed in two different contexts. The first source of observations on parental defense behavior is opportunistic observations of parental defense toward various potential predators that naturally entered the plot. Because potential predators are unpredictable and infrequent, these observations are necessarily anecdotal and subjective.

The second and primary source of observations comes from a series of experiments exposing all pairs to two potential predators, a ferret (*Mustela putorius*) and a black rat snake (*Elaphe*

obsoleta), on the 13th and 14th day after hatching of their chicks. Exposures to predators were conducted throughout the day, with tests at a given nest conducted on succeeding days at approximately the same time of day and experimental groups balanced for time of day. All trials were conducted in periods of no rain and moderate-to-warm air temperatures. Carnivores of the genus *Mustela* are important predators of hole-nesting birds (e.g., Perrins 1979), and the ferret was chosen as the nearest approximation to a native *Mustela* that was practical to keep in captivity. The ferret used was sandy-brown in color. Rat snakes are the most arboreal snake in northeastern North America, and they are important predators of arboreal nesting birds (e.g., Uhler et al. 1939). The black morph of rat snake is native to upstate New York, and we used a 2-m individual of this morph in 1986 and a 1.5 m individual in 1987 and 1988. In each season, only one of each type of predator was used. We had no indication that either predator changed its behavior over the course of the season in response to repeated exposure to swallows. Both predators were presented on leashes, with the snake attached to the floor of a box fixed to the top of a 0.85 m barrel and the ferret attached to the nest-box pole by a 0.9 m leash. These apparatuses were constructed after considerable experimentation to encourage approach of the predator toward the nest-box once its box was opened.

Predators were presented to all parents on successive days, with half the parents in each experimental group being exposed to the snake first and half to the ferret first. The presentations used the following protocol. Two hours before the predator trial began, a dummy version of the predator presentation apparatus (i.e., a box for the ferret and a barrel for the snake) was arranged at the nest-box in the same position and attitude that would be taken later by the apparatus containing the predator. One hour after the dummy was set out, an observer walked to the nest area, carrying a blind within which she/he was hidden. From a point about 12 m from the nest, the observer watched the progress of "normal" parental care at the nest, recording the arrivals and departures of each parent and their visible behaviors at the nest in coded form on a Tandy TRS 80 Model 100 Computer running an event-recorder program. After one hour, the predator handler walked to the nest with the apparatus

containing the predator. He/she installed the predator and its apparatus and left the immediate vicinity of the nest with the dummy. The observer in the blind had a fishing reel connected to a box-opening device on the predator apparatus. This activity required a total of about 8 min. The handler then took observations from a point approximately 50 m from the nest, paying particular attention to the identities of the birds in the nest area. The observer in the blind opened the box containing the predator when one of the parents entered the nest-box, or failing that, after seven minutes had elapsed. Fifteen minutes after delivering the predator in its apparatus, the handler returned to the nest and removed the predator and its apparatus, a process requiring about seven minutes. The observer remained in the blind and continued recording parental behaviors at the nest for one additional hour.

During each trial, we recorded alarm call rates on a four-point scale and numbers of dives by both the male and female at each nest (Table 1). These behaviors were recorded separately for the period while the handler first visited the nest, the predator trial itself, and the period while the handler returned to remove the predator. We also estimated the closest approach to the predator by both male and female swallow and the maximum number of swallows recruited to the anti-predator display during the predator trial. We later calculated the total time each parent was present during the trial, the duration of the periods of alarm-calling by each parent, and a series of latency measures for both parents. These latency measures represented the amount of time elapsed between the disappearances of the predator handler on his/her first visit and the reappearance of each parent within 10 m of the nest, the time elapsed between the predator's emergence and the reappearance of each parent, the time between the disappearance of the handler after his/her second visit and the reappearance of each bird, and the time between the handler's second departure and the landing of each parent back at the nest-box (Table 1).

STATISTICAL METHODS

Analyses were conducted with SYSTAT Version 4 (Wilkinson 1988a). Multivariate analyses of variance (MANOVAs) were conducted with the Multivariate General Linear Hypothesis procedure. MANOVAs allow an overall test of the ef-

fects of independent variables on all response variables combined. This overall test is complemented by univariate analysis of variance (ANOVA) tests for the effects of independent variables on each of the variables taken in isolation.

A cluster analysis to investigate the relationships among the various response variable was conducted using the CLUSTER module with Pearson correlation coefficients as the distance metric and the complete linkage (i.e., farthest neighbor) method (Wilkinson 1988a). For most response measures, it is reasonable to interpret larger values as indicative of more intense parental defense. Two broad exceptions are those measures of the closest approach of the defender to the predator and the latency to return to the nest after exposure to the predators or predator handlers. Entries in the correlation matrix involving these measures were adjusted in sign before running the clustering algorithm.

For multiple comparisons of similar measures conducted on the same set of birds, sequentially Bonferroni-adjusted P -values were used (Rice 1989). When large numbers of tests are conducted between the same two samples, some large differences are expected by chance and not because of real biological difference between the samples. The sequential Bonferroni adjustment remedies this by increasing the stringency of the criterion for rejection of the null hypothesis of no difference. This adjustment is performed by first ordering all the n candidate P -values from smallest to largest. The first P -value is compared to the traditional Bonferroni critical value of α/n . If smaller than this critical value, the null hypothesis is rejected. The test with the next largest P -value is then compared to a critical value of $\alpha/n-1$. If its P is smaller than this new critical value, the process continues, each time subtracting one from the denominator of the critical value, until a P -value is encountered that is larger than the appropriate critical value. Bonferroni adjustments require a subjective judgement by the researcher in choosing n , the number of comparisons over which the adjustment is to be applied. In this paper, I usually treat data from males vs. females and from defense toward handlers vs. toward predators as being "independent" and not in need of correction for multiple comparisons. In each set of multiple comparisons, the pool of measures over which I have conducted Bonferroni adjustments is indicated. I also present the unadjusted P -values for com-

parison. A significant difference is assumed to be one with an adjusted P -value ≤ 0.05 .

In some graphical plots in which a large number of points with identical values causes a large amount of the information to be lost, I "jitter" the plots (Wilkinson 1988b) by adding or subtracting a very small random number to x and y coordinates of each point, thereby allowing points with identical values to appear distinct. Curves fitted in such instances are based on the original data.

Rather than assuming a priori that trends are linear, I fit cubic splines to the data with the software of Schluter (1988). These algorithms find the path through the data which minimizes the sum of squared prediction errors for each point with the method of cross-validation (Schluter 1988). Thus, if the real trend is a curve, splines produce a curve that conforms more closely to the data than would a straight line. In all the splines presented here, I also present the splines representing ± 1 SE for each point, estimated with 200 iterations of the grid-search bootstrap method (Schluter 1988).

RESULTS

DESCRIPTION OF DEFENSE BEHAVIOR

The parental defense behavior of Tree Swallows is often intense. A human approaching a nest usually elicits the typical defense of this species. Parents emit a series of buzzy "Alarm" calls (see Robertson et al., in press) at rates sometimes exceeding two calls per second as they circle overhead. This is punctuated by a variable number of dives, each beginning with a climb to 5–20 m followed by a precipitate drop to within 0.5–2 m of the intruder. At the bottom of these dives, the parent often emits a soft "Rasping" or "Ticking Aggression" call (Robertson et al., in press) as it pulls out and steeply regains altitude. Occasionally, reaction to a predator is limited to simple whistled "Anxiety" calls (Robertson et al., in press).

Alarm-calling and diving are most often encountered during the period when a pair is actively occupying a nest. We have observed these behaviors, however, as early as 29 days before the first clutch initiation and as late as when adults were attending fledged chicks.

One of the challenges of observing parental defense behavior is recording all its various manifestations without missing any critical feature of

its variation. In this study, I tried to measure as many response variables as possible. This procedure holds hidden costs; however, in that many of the multiple measures recorded may be only slightly different ways of measuring the same behavior. In statistical analyses, I used multivariate techniques that avoid the problems of independence and reduced degrees of freedom that such multiple measures can cause. However, it is useful to understand how response variables are related.

To explore these connections, I conducted a cluster analysis on the correlations among the response variables for the entire data set. To test the generality of clustering patterns discerned, I separately analyzed the data for all first trials and second trials. In the resulting cluster diagrams (Fig. 1), the diagram for first-trial data is to the left and that for second-trial data is in mirror-image orientation to the right. The common set of response variables for both diagrams are arranged vertically between them. (The fact that the variables can be listed in the same order without violating the topology of the diagrams indicates considerable congruity between the two.) In these diagrams, correlations between pairs of variables are represented by the lengths of the paths along the diagram between them; longer paths denote weaker correlations. I have identified three clusters that are each united by a common linkage to one of three "branches" near the base of the "tree" (to the far left for the first diagram and the far right for the second). The first cluster includes the first nine variables on the diagram and consists entirely of male defense measures during the predator trial, the second includes the eight variables associated with defense by both sexes toward the predator handler before and after the trial, and the third consists of the nine variables associated with female defense. These three clusters have simple interpretations as "male," "handler," and "female" clusters, and the clustering at this level of discrimination is remarkably consistent in both trials, with the exception being the closer association of POSHFCAL with the female cluster in the second trial diagram. Thus, it appears there is more cohesion within individuals in their defense behavior than there is in types of behavior among members of a pair. Within each cluster there is further structuring of the response variables. For both sexes there is an "intensity" sub-cluster related to the intensity of response toward

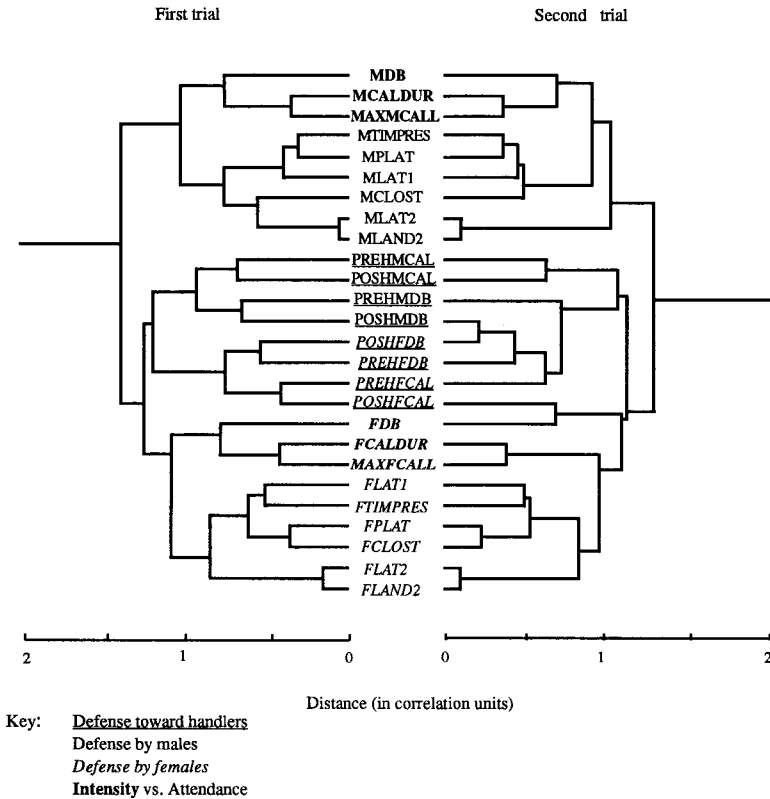


FIGURE 1. Cluster analysis of all defense measures for first and second trials taken separately. This diagram was constructed with the complete linkage method using Pearson correlation coefficients as the distance metric. The measures fall into three main clusters: one (consisting of the uppermost nine variables in the diagram) of male response measures to the predator, a second (the next eight variables in underlined text) of male and female responses to the predator handlers, and a third (the last 9 variables in italic text) of female response measures to the predator. Within the male and female clusters, the response variables are further structured into an "attendance sub-cluster" and an "intensity sub-cluster" (in bold text). Variable labels are given in Table 1.

the predator (i.e., rate and duration of alarm calling as well as number of dives) and an "attendance" sub-cluster involving the pattern of attendance at the nest during the trial (i.e., return latencies and time present). Within the handler cluster, male and female defense measures towards the handler tend to be separate, but correlations in these clusters tend to be weaker, and the patterns of correlation are not as comparable between the first and second trials. For both sexes, an unexpected result is that the closest approach to the predator is more closely clustered with the attendance sub-cluster than with the intensity sub-cluster. Note also that what would seem the most threatening aspect of defense (the number of dives toward the predator—MDB and FDB) is also the most variable and one of the least closely linked defense measures within both the male and female defense clusters (Fig. 1).

DETERMINANTS OF DEFENSE

Effects of repeated exposure to predator. Knight and Temple (1986a, 1986b) suggested that many reported seasonal increases in parental defense intensity could be attributed to the increased familiarity of the defending parent with the predator. This effect can be tested by comparing the reactions of parent swallows to handlers at the first and second predator trials. If the Knight and Temple effect were acting, birds should defend more strongly toward the predator handlers on the second trial. I analyzed the effect of order of presentation by assigning the dummy variable "order" the value of 1 for first trials, 2 for second trials and 3 for trials on pairs that abandoned or had their nests destroyed between the first and second trials. This last group consisted of 16 trials. Although MANOVA of all the defense vari-

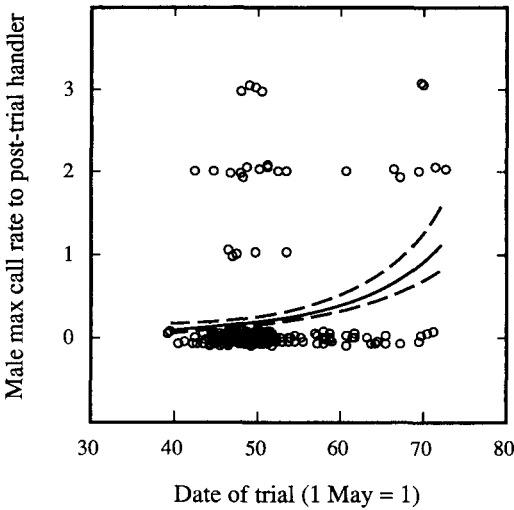


FIGURE 2. The effect of date of the predator trial on the maximal call rate of the male parent in response to the predator handler's visit at the end of the predator trial. Curve fit to data is a cubic spline ± 1 SE. For further details see text.

ables revealed a significant effect of order of presentation on defense (MANOVA Wilks' $\lambda = 0.689, F_{52,368} = 1.449, P = 0.029$), this effect was due to the trials with order = 3. When those nests are deleted, neither the MANOVA nor any of the individual ANOVAs are significant. Thus, there is no indication that the Knight and Temple effect is acting in Tree Swallows.

Effects of date. Montgomerie and Weatherhead (1988) suggested that intensity of parental defense should be lower in later nesting birds,

since the prospects for survival and subsequent reproduction of offspring are thought to decline with fledging date. Seasonal declines in the quality of individual breeders (cf. Stutchbury and Robertson 1988) could also lead to seasonal declines in defense. Alternatively, seasonally diminishing chances of reneating could lead to increased offspring value and increased defense (Weatherhead 1989). In any event, there is a slight but highly significant effect of date on defense behavior in the predator trials (MANOVA Wilks' $\lambda = 0.754, F_{26,184} = 2.312, P = 0.001$). This effect appears in only one defense variable (Tables 2 and 3): the male's maximal call rate (POSHMCAL) during the second visit of the handler. Males seem to invest more in defense as date increases (Fig. 2).

The effect of interannual differences. Each year has a unique set of daily values for weather and food, and these differences could lead to differences in parental defense behavior. There was a highly significant overall effect of year (MANOVA Wilks' $\lambda = 0.593, F_{52,368} = 2.111, P < 0.001$). Three of the significant univariate effects (Tables 2 and 3) involve female attendance, with more assiduous attendance in 1987 as evidenced by time present ($\bar{x}_{1986} = 302.2, \bar{x}_{1987} = 474.7, \bar{x}_{1988} = 365.7$), return latency after first handler ($\bar{x}_{1986} = 325.1, \bar{x}_{1987} = 167.6, \bar{x}_{1988} = 182.3$) and return latency after predator ($\bar{x}_{1986} = 292.3, \bar{x}_{1987} = 122.1, \bar{x}_{1988} = 169.6$). A similar pattern obtains for the males (Tables 2 and 3), with more time present in 1987 ($\bar{x}_{1986} = 389.0, \bar{x}_{1987} = 515.5, \bar{x}_{1988} = 355.1$), shorter return latency after first handler

TABLE 1. Measures of Tree Swallow response toward predators and predator handlers recorded in this study.

Measure	Abbreviation		Units	Range of values observed
	Male	Female		
Pre-trial dives toward handler	PREHMDB	PREHFDB	Count	0-32
Pre-trial maximum alarm-call rate toward handler	PREHMCAL	PREHFCAL	Subjective scale	0-3
Post-trial dives toward handler	POSHMDB	POSHFDB	Count	0-25
Post-trial maximum alarm-call rate toward handler	POSHMCAL	POSHFCAL	Subjective scale	0-3
Dives toward predator	MDB	FDB	Count	0-147
Closest approach to predator	MCLOST	FCLOST	m	0.15-100
Maximum alarm-call rate toward predator	MAXMCALL	MAXFCALL	Subjective scale	0-3
Duration of alarm calling during predator trial	MCALDUR	FCALDUR	sec	0-900
Pre-trial return latency after handler	MLAT1	FLAT1	sec	0-900
Post-trial return latency after handler	MLAT2	FLAT2	sec	0-3600
Post-trial latency to land after handler	MLAND2	FLAND2	sec	0-3600
Return latency after predator	MPLAT	FPLAT	sec	0-900
Time parent present during predator trial	MTIMPRES	FTIMPRES	sec	0-900

TABLE 2. Univariate analyses of variance for parental defense behavior toward predator handler.

Measure	Sex	Order effect (df = 2, 209)		Date effect (df = 1, 209)		Year effect (df = 2, 209)		Brood-size effect (df = 3, 209)		Predator effect (df = 1, 209)	
		F	P†	F	P†	F	P†	F	P†	F	P†
Return latency after 1st handler (LAT1)	Male	0.890	0.412	1.120	0.291	6.170	0.003*	0.109	0.955	0.052	0.821
	Female	5.794	0.004*	0.000	0.993	7.162	0.001*	1.522	0.210	0.100	0.752
Dives toward 1st handler (PREHDB)	Male	0.374	0.688	0.239	0.626	0.230	0.795	0.393	0.759	0.064	0.800
	Female	1.692	0.187	0.800	0.372	1.251	0.288	1.080	0.359	4.763	0.030
Maximum alarm-call rate toward 1st handler (PREHCAL)	Male	0.633	0.532	0.453	0.502	0.582	0.560	0.958	0.413	0.099	0.753
	Female	0.770	0.464	0.190	0.664	2.757	0.066	0.441	0.724	0.769	0.381
Dives toward 2nd handler (POSHDB)	Male	0.888	0.413	1.141	0.287	1.833	0.163	0.378	0.769	6.143	0.014
	Female	2.153	0.119	0.977	0.324	3.098	0.047	0.246	0.864	5.552	0.019
Maximum alarm-call rate toward 2nd handler (POSHCAL)	Male	0.154	0.857	10.342	0.002*	2.750	0.066	0.212	0.888	0.547	0.460
	Female	0.386	0.680	4.417	0.037	3.618	0.028	2.002	0.115	0.680	0.410

† These P -values are not adjusted for multiple comparisons. I have conducted sequential Bonferroni adjustments on these P -values, treating each effect independently and assuming there are five multiple comparisons to be adjusted in each sex. Those P -values with a sequentially adjusted P -value ≤ 0.05 are indicated with an asterisk. Although the overall significance of order, date, year, brood-size, and predator effects are best summarized by the multivariate P -values given in the text, the size of P -values presented here gives a relative indication of the strength of each predictor's effect on variation in each of the individual variables taken alone.

($\bar{x}_{1986} = 292.4$, $\bar{x}_{1987} = 158.6$, $\bar{x}_{1988} = 307.4$) and after the predator ($\bar{x}_{1986} = 249.3$, $\bar{x}_{1987} = 136.2$, $\bar{x}_{1988} = 232.9$). In addition, males in 1987 tended to approach the predator more closely ($\bar{x}_{1986} = 18.3$, $\bar{x}_{1987} = 6.5$, $\bar{x}_{1988} = 20.6$). I have gathered information on food supply, solar radiation, temperature, wind speed and precipitation (Winkler, in prep.). The only variable that is significantly different during the period of predator trials in 1987 compared to the analogous periods in 1986 and 1988 is solar radiation (ANOVA $P = 0.008$, $\bar{x}_{1986} = 40.760$, $\bar{x}_{1987} = 35.962$, $\bar{x}_{1988} = 50.275$), with 1987 being the cloudiest year of the trials.

Effect of brood size. Previous authors have reported inconsistent effects of changes in brood size on parental defense (reviewed in Montgomerie and Weatherhead 1988). Because my two experimental groups had reduced broods of one to three chicks and my control and non-experimental groups had normal broods of 5–6 chicks (Winkler 1991), I tested for the effect of brood size by comparing defense across all four treatment groups. All groups were balanced for initial clutch sizes. There was no significant effect of brood size (Tables 2, 3; MANOVA Wilks' $\lambda = 0.657$, $F_{78,551} = 1.066$, $P = 0.338$), indicating that it is not an important determinant of parental defense for these birds.

Effect of sex of defender. Many authors have suggested that intensity of parental defense should be related to the sex of the defender, since the relatedness of the parents to the offspring as well as the costs and efficacy of defense may be sex-specific (e.g., Trivers 1972, Curio 1980, Regelman and Curio 1983, Montgomerie and Weatherhead 1988). Comparisons of 13 defense measures between males and females indicate that the only significant differences are in maximal call-rate (MAXCALL) and call duration (CALDUR) during predator defense (Table 4). For both measures, the males display greater intensity of display than do the females (MAXCALL $\bar{x}_\delta = 1.036$, $\bar{x}_\varnothing = 0.692$; CALDUR $\bar{x}_\delta = 138.045$, $\bar{x}_\varnothing = 81.171$).

Effect of parental age. Some authors have suggested that parental age should affect parental defense intensity if there is an age-related decline in parental survivorship (e.g., Pugesek 1983; cf. Montgomerie and Weatherhead 1988). Another possible effect of age is that younger parents tend to produce fewer young (e.g., Stutchbury and Robertson 1988) and it would be interesting to know if young-parent effects extend to parental

TABLE 3. Univariate analyses of variance for parental defense behavior during predator trials.

Measure	Sex	Order effect (df = 2, 209)		Date effect (df = 1, 209)		Year effect (df = 2, 209)		Brood-size effect (df = 3, 209)		Predator effect (df = 1, 209)	
		F	P†	F	P†	F	P†	F	P†	F	P†
Dives toward predator (DB)	Male	0.114	0.892	0.079	0.778	3.189	0.043	1.710	0.166	7.595	0.006*
	Female	0.143	0.867	0.638	0.425	0.188	0.829	1.038	0.377	4.043	0.046
Closest approach to predator (CLOST)	Male	0.324	0.723	0.880	0.349	5.573	0.004*	0.491	0.689	0.005	0.945
	Female	14.228	<0.001*	2.466	0.118	3.035	0.050	0.139	0.937	0.264	0.608
Maximum alarm-call rate toward predator (MAXCALL)	Male	0.617	0.541	0.113	0.737	1.760	0.175	1.148	0.331	11.427	0.001*
	Female	0.685	0.505	0.130	0.719	2.908	0.057	0.910	0.437	0.371	0.543
Duration of alarm calling during predator trial (CALDUR)	Male	0.626	0.536	0.025	0.874	4.210	0.016	0.402	0.752	12.419	0.001*
	Female	0.273	0.762	0.017	0.897	0.278	0.757	0.547	0.651	2.385	0.124
Return latency after 2nd handler (LAT2)	Male	1.148	0.319	1.294	0.257	3.011	0.051	3.904	0.010	0.013	0.910
	Female	7.957	<0.001*	7.271	0.008	0.940	0.392	0.635	0.593	0.056	0.814
Latency to land after 2nd handler (LAND2)	Male	0.557	0.574	2.015	0.157	3.323	0.038	3.170	0.025	0.218	0.641
	Female	4.616	0.011	3.754	0.054	1.980	0.141	0.076	0.973	0.040	0.843
Return latency after predator (PLAT)	Male	1.150	0.319	3.967	0.048	5.301	0.006*	0.612	0.608	0.466	0.496
	Female	5.201	0.006*	0.645	0.423	9.191	0.000*	0.051	0.985	0.239	0.626
Time parent present during predator trial (TIMPRES)	Male	1.911	0.151	0.799	0.372	5.473	0.005*	0.870	0.458	3.104	0.080
	Female	2.150	0.119	0.000	0.997	6.879	0.001*	0.933	0.426	7.064	0.008

† These P-values are not adjusted for multiple comparisons. I have conducted sequential Bonferroni adjustments on these P-values, treating each effect independently and assuming there are eight multiple comparisons to be adjusted in each sex. Those P-values with a sequentially adjusted P-value ≤ 0.05 are indicated with an asterisk. Although the overall significance of order, date, year, brood-size, and predator effects are best summarized by the multivariate P-values given in the text, the size of P-values presented here gives a relative indication of the strength of each predictor's effect on variation in each of the individual variables taken alone.

TABLE 4. Independent samples *t*-tests comparing parental defense variables during predator trials for males and females. Sample sizes are indicated for the sex with the fewest values in the analysis. Of these nine comparisons, those comparisons with a sequentially Bonferroni-adjusted *P*-value of <0.05 are indicated with asterisks. Variable labels are given in Table 1.

Variable	<i>n</i>	Male average	Female average	<i>t</i>	Pooled variance <i>t</i>	<i>P</i>
DB	224	2.647	1.496	-1.329		0.185
CLOST	222	14.706	10.855	-1.310		0.191
MAXCALL	224	1.036	0.692	-3.404		0.001*
CALDUR	222	138.045	81.171	-3.100		0.002*
LAT1	223	247.646	211.969	-1.332		0.184
LAT2	224	585.420	415.277	-2.138		0.033
LAND2	224	741.089	562.746	-2.213		0.027
PLAT	222	200.507	182.009	-0.828		0.408
TIMPRES	220	423.652	391.205	-1.149		0.251

defense. Unfortunately, I do not have sufficient numbers of known-aged individuals to test this possibility in males. In females, age was determined by banding records and the age-related plumage sequence (Hussell 1983). In females, there is no significant effect of female age on defense intensity using any combination of the 13 female defense variables (MANOVA Wilks' $\lambda = 0.944$, $F_{13,136} = 0.623$, $P = 0.832$).

Effect of parental condition. Wallin (1987) reported that parental defense in the Tawny Owl (*Strix aluco*) varies with the condition of the defending parent, and such relations are intuitively appealing because parental condition presumably affects the relative costs and effectiveness of parental defense. To investigate this effect, I computed a condition index for each bird, defined as the difference between its mass and a mass predicted from its wing length. (I assume that condition affects wing length much less than mass.) Predicted mass was determined by linear regression ($R^2 = 0.044$, $P < 0.001$) from a sample of 1,178 measurements taken on swallows at the Ithaca field site over the years 1985 through 1989. The predicted weight in grams (\hat{w}) is given by the equation:

$$\hat{w} = 8.383 + 0.110C$$

where *C* is the length of the flattened and straightened outer wing "chord" (see Svensson 1984) in mm. For the analysis of condition's effect on defense, I included only those birds for which I had a mass measurement within six days of one of the predator trials.

Although the overall MANOVA results for females are non-significant (Wilks' $\lambda = 0.884$, $F_{13,116} = 1.171$, $P = 0.310$), the univariate test for FPLAT was significant (Bonferroni $P = 0.026$). (This sit-

uation can arise when there is a small number of significant effects that are not strong enough to overcome the enormous cost in degrees of freedom entailed in the *F*-values for MANOVA.) The significant univariate test in this case indicates that females in better condition return sooner after their exposure to the predator (Fig. 3). I found no significant effect of condition on parental defense for males (MANOVA Wilks' $\lambda = 0.917$, $F_{13,125} = 0.876$, $P = 0.580$).

Effect of other individual differences. To test for consistent differences between individuals in defense, I compared responses toward the predator handler in the two trials conducted each year on each nest. Of the correlations of ten measures taken on males and females for reaction to the predator handler, four are significant. These correlations indicate that males tend to have similar call rates toward handlers retrieving the predators on the first and second trials ($r_s = 0.39$, $P < 0.001$, $n = 119$). Also, the return latencies for both the males and females after the pre-trial visit of the handler tend to be similar on the first and second trials (males: $r_s = 0.26$, $P = 0.005$; females: $r_s = 0.37$, $P < 0.001$). Finally, females dive toward the handler delivering the predator with similar intensities on the first and second trials ($r_s = 0.48$, $P < 0.001$). I interpret these data as providing reasonably strong evidence for consistent individual differences in defense behavior.

Effect of defense by mate. From the perspective of life history theory, one of the most interesting aspects of parental defense behavior is that it is predicted to be responsive to the defense effort of the mate (e.g., Winkler 1987). Few studies have documented such effects, but those that have report cooperation between pair members (Curio

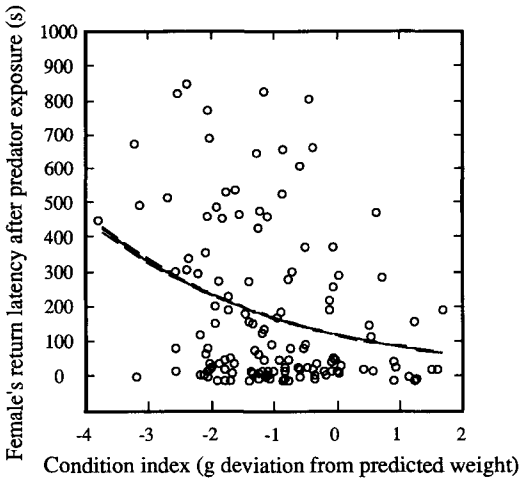


FIGURE 3. The relation between the female's condition index (see text) and her latency to return to the nest area after having been exposed to the predator. The curve through the points is a cubic spline ± 1 SE. For further details see text.

and Regelmann 1985, Regelmann and Curio 1986, Weatherhead 1989).

Cluster analysis (Fig. 1) indicates that the defense behavior of the male and female are not very closely related, but it is instructive to examine those correlations between them that are significant (Table 5). Males and females tend to return to the nest after a disturbance at about the same time, thus their return latencies (i.e., LAT1, LAT2, PLAT) are correlated positively (Table 5, Fig. 4A). They also tend to remain (i.e., TIMPRES) for similar lengths of time (Fig. 4B) and to approach the predator to similar distances (CLOST; Table 5). Because parents that return early (i.e., have short return latencies) have more potential time to spend at the nest, return latencies tend to be negatively correlated with time present (Table 5).

Two interesting patterns are revealed by the correlations between mates in the intensity cluster of behaviors. First, all but one (Fig. 4C) of the significant correlations among responses occur for responses to the predator handler, not the predator. Second, the distributions of responses in the intensity cluster are distinctive. While the correlations of attendance variables seem to result from a fairly consistent trend across pairs of mates (e.g., Fig. 4A and B), those in the intensity variables result from a dichotomy in the kinds of responses that pairs express. In some, there is unanimity of response, with both members of a pair either doing nothing (quite common) or both

exerting considerable defense (rare). In other pairs, one or the other of the pair defends whereas the other does nothing (Fig. 4C and D). Some significant correlations are for diving before and after the trial (e.g., Fig. 4D, Table 5), suggesting that the members of pairs may be "trading off," with one diving most before the trial and the other diving vigorously after the trial. This is unlikely, however, because diving toward the handler before and after the trial are positively correlated in both males ($r_s = 0.281$, $P < 0.001$, $n = 224$) and females ($r_s = 0.352$, $P < 0.001$, $n = 224$).

Effect of type of predator. Many authors (e.g., Kruuk 1964, Curio 1975, Patterson et al. 1980, Buitron 1983, Walters 1990) presented evidence that defending parents make distinctions among the types of predators threatening their offspring and adjust their parental defense accordingly. The results of the MANOVA indicate that Tree Swallows do this as well. There is a significant overall effect of predator type on parental defense behavior during the predator trials (Wilks' $\lambda = 0.806$, $F_{26,184} = 1.706$, $P = 0.023$). Individual defense measures differing most in response to predator type (Table 3, Column 5) are male diving rate (MDB: $\bar{x}_{\text{ferret}} = 4.64$, $\bar{x}_{\text{snake}} = 0.62$), maximal male call rate (MAXMCALL: $\bar{x}_{\text{ferret}} = 1.30$, $\bar{x}_{\text{snake}} = 0.77$), male call duration (MCALDUR: $\bar{x}_{\text{ferret}} = 189.74$, $\bar{x}_{\text{snake}} = 85.41$), and the amount of time the female was present during the predator trial (FTIMPRES: $\bar{x}_{\text{ferret}} = 437.96$, $\bar{x}_{\text{snake}} = 343.59$). All of these show greater intensity of responses toward the ferret than toward the snake.

Considering the predator handlers in the trials as potential predators, the parent's behavior toward the handlers can be compared with their behavior toward the two predators. Both maximal alarm call rates and rates of diving were higher toward real predators than toward the handlers, with the effect being more highly significant in males than in females (Table 6). This effect cannot be ascribed to the timing of exposure, since the differences were as strong comparing predator defense with defense against the handler either before or after the predator trial. In addition, defense toward the handler before and after the trial did not differ (Table 6).

Observations of the reactions of parents to various potential predators encountered in the natural course of the breeding season are also relevant here (Table 7). In interpreting the overall magnitude of defense, both the frequency and intensity of the response must be included. For

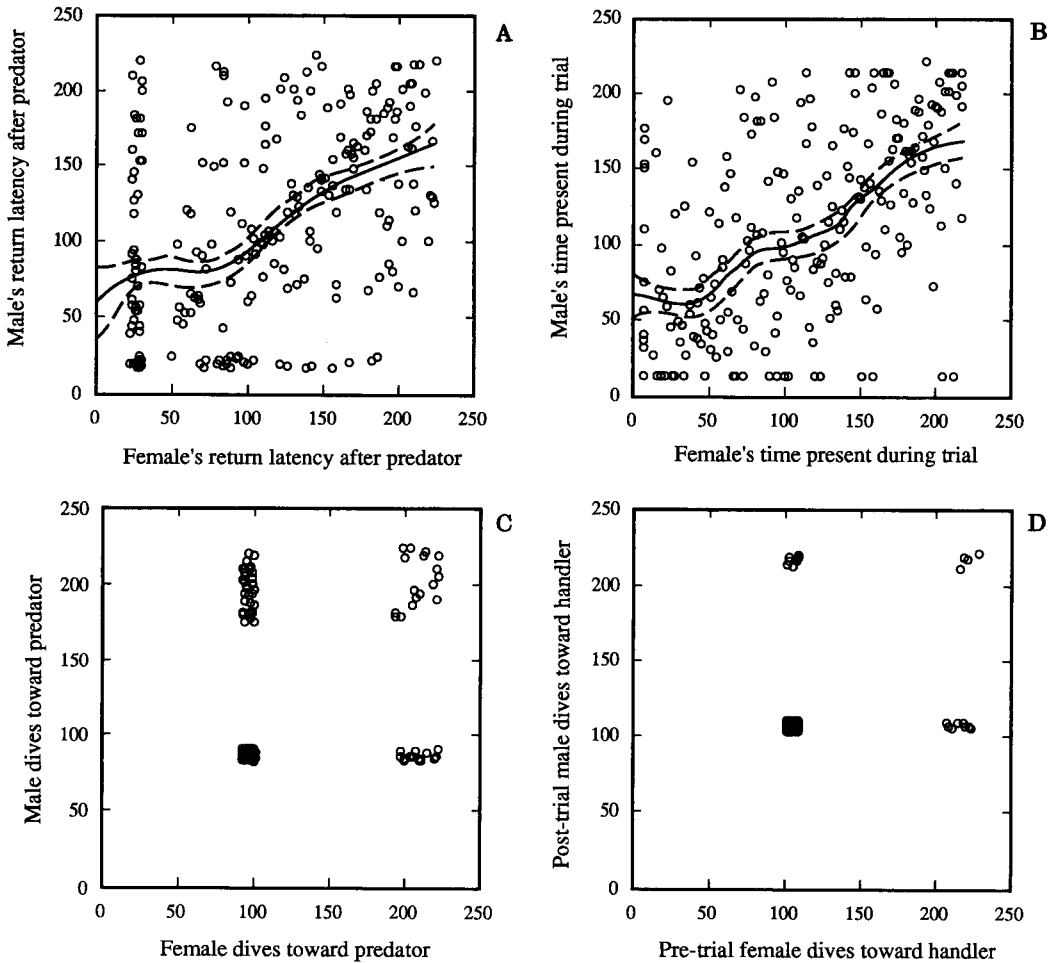


FIGURE 4. Plots of significant relations between a parent's defense performance and that of its mate: (A) Male's return latency after exposure to the predator vs. the same latency for the female; (B) Male's time present near the nest during the predator trials vs. the time present by the female; (C) Male's dives toward the predator vs. those for the female; (D) Male's dives toward the handler after the trial vs. female's dives toward the handler before the trial. The values in these plots are ranks and the curves in (A) and (B) are cubic splines ± 1 SE. The large dark symbols in the lower left of (C) and (D) result from the superimposition of a very large number of data points with no defense by either parent. The bimodal distributions of points in these latter two plots are such that splines do not aid the perception of trends.

instance, many swallow pairs interact with *Agelaius* on a daily basis, but rarely defend against the blackbird. Indeed, the intensity of defense, once expressed, is considerably more consistent than is the frequency of its expression, and a meaningful impression of overall reaction to a species can only be gained by considering both. For the species with which Tree Swallows rarely interact, I have declined to make even a subjective estimate of their frequency of defense.

Two hole-nesting species require more explanation. European Starlings (*Sturnus vulgaris*) are

common in the study area, but they do not often interact with swallows because our boxes are constructed with holes too small to admit starlings. On the one occasion when a starling was observed to investigate boxes, it was dived at and eventually chased off by one of the resident birds. Presumably, the frequency and outcomes of such encounters would be different if starlings were able to enter the boxes.

House Sparrows (*Passer domesticus*) commonly visit the area to initiate nesting in the boxes erected for swallows. When a sparrow lands

TABLE 5. Spearman correlations between the defense measures of males (rows) and females (columns). The correlations are presented separately for the "attendance" cluster of behaviors and the "intensity" cluster (for distinction see text). I conducted sequential Bonferroni-adjustments separately for the 36 attendance correlations and the 49 intensity correlations. The sample size for each of these correlations is 219. Those correlations with an adjusted *P* value of <0.05 are indicated with an asterisk. Variable labels are given in Table 1.

	CLOST	TIMPRES	PLAT	LAT1	LAT2	LAND2	
CLOST	0.255*	-0.323*	0.244*	0.192	0.142	0.059	
TIMPRES	-0.085	0.547*	-0.336*	-0.306*	-0.161	0.037	
PLAT	0.128	-0.355*	0.435*	0.225*	0.067	-0.006	
LAT1	0.080	-0.353*	0.236*	0.399*	0.121	0.001	
LAT2	0.093	-0.247*	0.093	0.112	0.368*	0.058	
LAND2	0.104	-0.138	0.078	0.114	0.108	0.178	
	PREHDB	POSHDB	DB	PREHCAL	POSHCAL	MAXCALL	CALDUR
PREHDB	0.226*	0.142	0.090	0.216	0.080	0.003	0.010
POSHDB	0.268*	0.491*	-0.096	0.275*	0.243*	-0.059	-0.041
DB	-0.055	-0.083	0.310*	-0.079	-0.079	0.164	0.159
PREHCAL	0.102	0.031	0.096	0.008	-0.029	0.161	0.153
POSHCAL	0.012	0.111	-0.008	-0.018	0.109	0.085	0.095
MAXCALL	-0.008	-0.076	0.133	-0.067	-0.113	0.043	0.088
CALDUR	-0.043	-0.071	0.108	-0.093	-0.079	0.046	0.087

on or near a box occupied by swallows, it is usually dived upon and aggressively harassed by both members of the resident pair if they are present. Often, if the sparrow succeeds in gaining entry to an active but temporarily unoccupied box, it is pursued inside by the resident swallow pair upon their return and usually forcefully evicted. Most interactions with sparrows at swallow-occupied boxes result in the sparrow being chased away. However, there have been at least three instances in which adult swallows have been killed in their boxes when available evidence pointed to House Sparrows as the cause of death. A sparrow apparently can kill an adult swallow if it

enters a box and finds a lone swallow inside. Apparently, by blocking exit from the box, it can repeatedly peck the swallow in the head and eventually kill it. Sparrows are also implicated in several cases of destruction of eggs and killing of broods of chicks.

When House Sparrows enter nests not used in that season by swallows, they usually do so unchallenged by neighboring swallows. Interactions between swallows and sparrows most often take place when sparrows begin to show interest in boxes adjacent to those in which they have built a nest unchallenged.

Swallows also react to raptors. All of the de-

TABLE 6. Paired samples *t*-tests for diving and calling behavior toward predators and toward predator handlers. These analyses based on a sample of 224 predator trials. I conducted separate Bonferroni-adjustments for the six comparisons for each sex, and those comparisons with an adjusted *P*-value of <0.05 are indicated with an asterisk. Variable labels are given in Table 1.

Sex	Variables compared	Mean difference	<i>t</i>	<i>P</i>
Male	PREHDB vs. POSHDB	0.192	0.935	0.351
	PREHDB vs. DB	-2.009	-2.653	0.009*
	POSHDB vs. DB	-2.201	-2.867	0.005*
	PREHCAL vs. POSHCAL	0.027	0.517	0.605
	PREHCAL vs. MAXCALL	-0.754	-9.910	<0.001*
	POSHCAL vs. MAXCALL	-0.781	-9.977	<0.001*
Female	PREHDB vs. POSHDB	0.080	0.504	0.615
	PREHDB vs. DB	-1.013	-2.061	0.040
	POSHDB vs. DB	-1.094	-2.294	0.023
	PREHCAL vs. POSHCAL	0.058	1.247	0.214
	PREHCAL vs. MAXCALL	-0.496	-6.549	<0.001*
	POSHCAL vs. MAXCALL	-0.554	-7.835	<0.001*

TABLE 7. Summary of field observations of defensive behavior. Only species toward which some defense has been observed are presented here. There are many other species (e.g., *Branita canadensis*, *Butorides striatus*, *Quiscalus quiscula*, *Turdus migratorius*) with which the swallows regularly come into contact and against which defense has never been observed.

Target species	Frequency of interaction	Frequency of defense	No. of defense bouts observed	Intensity of defense	Risk to parent	Risk to offspring	Reaction of target to defense
<i>Agelaius phoeniceus</i>	Very high	ca. 5%	ca. 100	high; mostly individual	0	0	slight; eventual departure after ca. 1 min
<i>Mimus polyglottos</i>	Rare	?	1	high; group	0	0	departure
<i>Melospiza melodia</i>	Common	Rare	1	high; individual	0	0	departure
<i>Corvus brachyrhynchos</i>	Common	ca. 10%	ca. 50	high; usually individual, some group	0	slight	none; departure after swallow
<i>Sturnus vulgaris</i>	Rare*	?	1	high; individual	0	slight/moderate	eventual departure
<i>Passer domesticus</i>	Fairly common	ca. 80%	ca. 30	high; individual	moderate if in box	high	eventual departure if not already established in neighboring box—see text
<i>Ceryle alcyon</i>	Occasional	ca. 10%	2	high; pair	0	0	gaping, ducking, crest-raising; departure
<i>Colaptes auratus</i>	Rare	?	1	high; group	0	0	departure
<i>Falco sparverius</i>	Uncommon	>90%	48	very high; both individual and group	slight	high	very slight duck occasionally; departure after swallow
<i>Falco columbarius</i>	Rare	?	1	very low; only whistled alarm calls from afar	high	moderate?	departure after swallow; continued flying unimpeded
<i>Accipiter</i> sp.	Uncommon	>90%	3	high; mob	moderate	moderate?	usually rushed departure

* Holes of nest boxes too small for starlings—see text.

fense toward American Kestrels (*Falco sparverius*) was seen when the falcon was perched. The only interaction observed with Merlins (*Falco columbarius*) occurred when one flew over the study area at an altitude of about 30 m on 17 April 1989. The swallows gave whistled alarm calls (apparently the "Anxiety" call of Robertson et al., in press) in response to the Merlin's passage, but none gave chase to mob it. Interactions with *Accipiter* hawks were always short. *Accipiters* flying across the study area are mobbed by groups of 15–50 swallows, and a perched *Accipiter* in the area is soon driven off by mobbing birds. We have only once seen a swallow dive toward an *Accipiter*.

ADVANTAGES OF DEFENSE

A critical assumption of studies of nest defense in birds has been that variation in the behavior is reflected in variation in the threat of predation of the nest. Our observations suggest that the advantages of defense may be very small. In over 200 trials conducted over three years using both the ferret and the snake, we saw no evidence that parental defense behavior would likely dissuade these predators. We never saw the rat snake respond aversively to the calls or dives of the swallows. On the infrequent occasions when the ferret responded to the swallows' defense behavior, the response was that he usually jumped into the air toward the diving birds, seemingly more attracted and excited than rebuffed. Similar lack of reaction typifies the response of crows and kestrels to defense behavior by the swallows (Table 7).

DISCUSSION

THE DETERMINANTS OF PARENTAL DEFENSE BEHAVIOR

The effect of the parent's sex on calling behavior during the predator trial is one of the few significant effects observed in this study. It is interesting that males call longer and more vigorously than do females (cf. Weatherhead 1989), especially since it is likely that males have lower certainty of paternity than do females (Lifjeld et al., in press). It is unlikely that calling, as compared to diving, carries a very high cost in either risk or metabolic expenditure. There is no sex-difference in calling behavior in response to predator handlers, and this counter-intuitive response to predators may reflect males being more aggressive in territorial defense (e.g., Robertson

et al., in press) and may thus respond more intensely to a novel threat near the nest.

Interannual differences were also significant in affecting parental attendance patterns, though it is difficult to understand how cloudiness would affect attendance. Further investigations of environmental determinants of parental defense are warranted. It may be that explanations of interannual differences should also be sought in conditions on the wintering grounds.

The final factor clearly affecting variation in parental defense behavior is the identity of the predator. Ferrets elicited a greater response from the males in both diving and calling behavior, while females stayed in the nest vicinity longer when in the presence of the ferret.

FUNCTION OF DEFENSE IN TREE SWALLOWS

To better understand the costs and benefits of parental defense and the selective factors that may have molded this behavior in the past, it is important to understand the function of defense behavior in this species. The first question to be answered is who or what, if anything, is being defended. Shields (1984) concluded that active parental defense in Barn Swallows (*Hirundo rustica*) entailed defense of offspring and possibly the mate, but not self-defense or defense of adjacent collateral kin. By contrast, passive defense (i.e., simple "mobbing") could be interpreted most straightforwardly as self-defense.

Another possible function of defense is defense of a nest-site (Windsor and Emlen 1975), as this is likely to be a limiting resource in most Tree Swallow populations. This may help explain defense against House Sparrows as well as explain the single instances of defense observed against starling and flicker.

If Tree Swallow active defense is viewed as serving primarily to defend offspring or the nest-site, the next question is how the parent's actions during active defense might lessen the risk of the offspring being preyed upon or the nest lost. For a species that engages in active defense, there seem to be only four likely hypotheses (cf. Curio 1978). The defender could be frightening the predator/competitor away with the threat of physical injury. In the case of the Tree Swallow, this would appear to be a real threat only for the very smallest predators/nest competitors (e.g., House Sparrow). This may be the only mechanism relevant for nest competitors, since animals

too large to be intimidated by swallows are likely too large to use their nest-holes. Indeed, most larger predators showed very little inclination toward immediate flight as a response to swallow defense. The second possibility is that the swallows, through their defense, are attracting larger predators that could in turn prey upon the predator/competitor threatening the swallows' nests (Levin et al. 1977, Bourne 1977, Curio 1978). Predators capable of threatening the potential predator of a bird's nest will often themselves constitute a threat to the nest (Montgomerie and Weatherhead 1988). In temperate North America, there would appear to be no large predators that would threaten smaller predators without in turn threatening the nest being defended. The third possibility is that the defense behavior of the swallows could serve to move the predator on (Curio 1978, Buitron 1983). Interestingly, the larger predators that seemed most likely to leave when defended against were those that prey upon birds. The swallows may be alerting the predator that it has been observed, that all birds in the vicinity have been alerted, and that foraging in the area is thus a waste of time. Furthermore, the speed with which the predator is attacked may indicate to a learning predator that future attempts to attack undetected will likely fail. Those predators that were preying on microtines (kestrel) or invertebrates (crows, blackbirds) or not foraging at all (blackbirds) were generally slow to leave the area in response to the birds' attacks, perhaps because their foraging success would not be impaired by the presence of an alert, predator-aware neighborhood of swallows. A problem with this interpretation is that a predator preying on nestlings should not concern itself with the alertness of the parents. This leads to the final, and equally likely, possibility that the swallows' defense behavior serves merely to distract the predator until it moves on. If birds are defending against mobile predators, the best defense may simply be to distract the predator from the nest until it is driven by its internal motivation to move on. Although the swallows show no behavior that would lead the predator away from the nest, observations of the ferret jumping at diving birds suggest that parents can distract a predator.

In this paper, I have focussed on the active defense components of the swallows' anti-predator behaviors. However, it is interesting that passive components of their behavior may serve

to reinforce the defense function of neighboring birds' displays. The number of swallows circling above a defending pair is strongly affected by the intensity of the pair's defense (Winkler, in prep.), indicating that a pair can increase the visual (and, to a lesser degree, auditory) impact of their defense with the help of their neighbors. Birds joining mobbing aggregations incur little risk in doing so because they remain quite distant from the predator. However, they benefit substantially if increasing the size of their aggregation increases its informative power.

If one of the functions of defense behavior is to distract large predators or inform them of poor prospects for foraging, how might this explain differences in defense intensity expressed toward the snake and ferret and toward the various bird species observed non-experimentally (Table 7)? Variation in either costs or benefits could affect the intensity of defense, and both appear to be important. Both mustelids and snakes are probably moderate threats to parent swallows, and they probably both are a great threat to swallow nestlings. But the audible components of defense are likely to be much less effective against snakes than against mustelids, since the former probably cannot hear. I suggest that this reduced efficacy of auditory defense against snakes and the resultant reduced benefits from defense might explain the difference in defense intensity observed toward these two predators.

Consideration of the benefits of defense explains some of the variation in behavior observed toward birds. Kestrels and *Accipiters* are probably both minor threats to adult swallows on the wing, but kestrels are attacked more aggressively. This may be because, unlike *Accipiters*, they are hole-nesters (and thus potential competitors for nest-holes) as well as a threat to swallow nestlings (Freer 1973, Windsor and Emlen 1975, Wilkinson and English-Loeb 1982). Similarly, the House Sparrow is attacked most often of all passerines, and probably comprises the greatest threat to nestlings and nest-site.

Costs of defense also seem important. Merlins and *Accipiters* probably both comprise small or moderate threats to nestlings. However, Merlins are certainly a much greater threat to adult swallows on the wing, and this may explain the low intensity of response observed toward the latter species.

Other species defended against may be remote threats to nest-site (flickers) or offspring (e.g.,

crows). The mockingbird may actually have been attacked because of resemblance to a rare potential nestling predator, the Loggerhead Shrike (*Lanius ludovicianus*). Some species, however, (e.g., sparrow, blackbird, kingfisher) are unlikely to be a threat. It may be that defense against these species is a carry-over from defense toward other species to a situation with negligible parental risk.

WHY FEW VARIABLES ARE SIGNIFICANT DETERMINANTS OF DEFENSE

Although the sex of the defending parent and the type of predator had clear effects on the defense behavior of Tree Swallows, it is remarkable that many other variables had little or no effect. This failure to detect more significant determinants of defense is probably not an artifact of my methods. The predators used in these experiments are either known to be important predators of bird nests or to closely resemble forms that are. I recorded a very large number of response variables to describe parental defense, and it is unlikely that a key element of defense was omitted that would be distinctively affected by the determinants I measured. Furthermore, the variables measured were recorded with sufficient accuracy and precision to reveal large variations between parents in their defense. I do not believe that significant effects were missed because of measurement error.

Positive correlations between members of a pair in their patterns of attendance at the nest during the predator trials (Table 5, Fig. 4) indicate that the attendance of a parent is positively affected by that of its mate. This indication of cooperation among the members of a pair is countered, however, by the presence of only one significant correlation among the intensity measures in response to a predator. All other correlations that exist in the intensity measures are in responses to the predator handlers. Despite the reported observations of cooperation in parental defense (Curio and Regelmann 1985, Regelmann and Curio 1986, Weatherhead 1989), it is not clear that a positive correlation should be expected, since both members of the pair would presumably have much to gain if their mates engaged in the risky behaviors of defense while they refrained from defense and observed the defense in relative safety in the circling mob of their neighbors. Indeed, I suggest that pairs have positive correlations in their attendances because

they are monitoring each other to see who will first abandon restraint and begin active defense in response to any given predator. This interpretation is reinforced by the large number of pairs observed in which one parent is expending active defense while the other is doing nothing (Fig. 4C and D).

Another variable with equivocal effect on parental defense is female condition. Most multivariate analyses of variance (MANOVA) that yield insignificant overall *P*-values for the effect of a predictor variable had insignificant *P*-values for the effects of that predictor variable on each of the response variables taken individually. The exception was the test for the effect of female condition. In this analysis, there were significant effects of female condition on female return latency after exposure to the predator (Fig. 3) and possibly on the amount of time spent near the nest during the trial. This observation reinforces that of Wallin (1987) on Tawny Owls, and the presence of a condition effect in such disparate taxa suggests that such effects should be investigated in greater detail and in a broader variety of species.

Although date had a significant effect on one measure of response to the predator handler when he/she was retrieving the predator (Fig. 2), this effect is difficult to interpret. Increases in defense with date have been predicted in response to declining re-nesting potential (Weatherhead 1989). However, this interpretation cannot explain the observed seasonal increase in Tree Swallows because this species is single brooded and re-nesting potential has fallen to essentially zero by the time most nests have reached the stage at which the predator trials were conducted in this study. Further progress in understanding the effect of date requires elaboration of predictions based on measured seasonal changes in the probabilities of relaying and offspring recruitment.

In my data, I find no support for the effect of repeated exposure to the predator, reinforcing the negative results of McLean et al. (1986) and Weatherhead (1989) attempting to verify the effect reported earlier (Knight and Temple 1986a, b). The lack of an effect of female age on parental defense is perhaps not surprising, as we would not expect such an effect in a species in which survival rates are essentially age-independent (Montgomerie and Weatherhead 1988, Weatherhead 1989). It is interesting, however, that the

effect of female age on clutch size and offspring production (Stutchbury and Robertson 1988) does not extend to effects on parental defense.

There is no effect of changes in brood size on parental defense, contrary to theory (e.g., Winkler 1987, Redondo 1989) that predicts that defense should decrease with decreasing brood size if defense has any costs at all. Despite this apparent contradiction of theory, it is interesting that previous studies of defense have found equivocal effects of variation in offspring number (reviewed in Montgomerie and Weatherhead 1988). In the Tree Swallow, this lack of brood-size effect is clearly not a case where the swallows cannot monitor the contents of their nests, as their abandonment frequency is quite responsive to changes in offspring number (Winkler 1991). One possible explanation is that the costs and benefits of parental defense are strongly non-linear, approaching a threshold step-function, such that any defense may carry very similar costs *and* benefits, no matter how many offspring are being defended.

VARIABILITY OF DEFENSE

Although sample sizes and control of possible determining factors were greater in this study than in many other studies of parental defense, it is possible that I failed to detect a larger number of significant determinants of parental defense merely because defense behavior is so variable. While this explanation may help explain my findings, it raises the larger question of why defense is so variable. Patterson et al. (1980), Buitron (1983) and Reid and Montgomerie (1985) stressed that variable defense behavior should be variable over time, but the variability that I observed in this study was obtained within only a two-day window at the same stage of nestling development for all nests studied. Such variability is especially unexpected in parental defense behavior because a predator poses an immediate and potentially fatal threat to the nestlings that would seem to require a response that cannot be postponed (Wallin 1987).

There are two possible explanations for this variability. The first explanation views the variability *per se* as an adaptation (Montgomerie and Weatherhead 1988). Most species have a threshold distance of the predator from the nest above which they will not defend the nest, and in many (including the Barn Swallow [Shields 1984]) the

intensity of defense increases as the predator approaches the nest within this threshold distance. Such behavior can aid naturalists in locating cryptic nests, and Montgomerie and Weatherhead (1988) highlighted the paradoxical nature of such behavior, suggesting that variability in defense intensity may serve to counteract this effect. Viewing Tree Swallows nesting in nest-boxes, it is tempting to dismiss this possibility as an explanation for defense variability in this species, since any predator could presumably locate the nest with little difficulty. But the natural cavities in which Tree Swallows appear to have nested in pre-colonial times (e.g., Rendell and Robertson 1989) often occur in dense stands of dead trees, many with multiple nest holes (Winkler, unpubl.). Thus, it is possible that the variability in parental defense observed today remains from a period when such variability may have diminished information on nest-location passed to the predator. Further acceptance of this possibility must await a more thorough analysis of the problem, however, because the hypotheses are too complicated to resolve with simple verbal arguments.

To the extent that parental defense is largely distractive in function, variability in response could be adaptive in preventing potential predators from habituating to the defense behavior. Here, too, a more careful theoretical and experimental analysis of this potential adaptive function is needed.

The other possible explanation for the extreme variability of parental defense in the Tree Swallow is that the benefits or costs of defense are not sufficiently large to have allowed selection in this species to have finely tuned the level of defense. Thus, while it seems clear that defense against such species as the House Sparrow is advantageous, the variable, and sometimes considerable, intensity of defense directed toward other larger species could be a transferred effect that has not been selected against. Similarly, the more intense defense displayed by males may be a correlate of selection for strong territorial defense. The lack of selection for fine adjustment in these behaviors in other contexts could be due to low effectiveness and costs of defense *per se*. Alternatively, because of the relatively short life-span of the swallow, encounters with predators may be so infrequent that selection has not been able to act effectively in narrowly adjusting their expression (Reeve and Winkler, in prep.).

ACKNOWLEDGMENTS

This research was funded by a grant from the Whitehall Foundation and an NSF Postdoctoral Fellowship in Environmental Biology. Some analyses were made possible with support from the USDA (Hatch Project No. 183-428). The field work was made possible through the dedicated assistance of Fred Adler, Monica Bosworth, Mike Clark, Kurk Dorsey, Peter Kleinman, Shai Mitra, Randy Moore, Cynthia Schiefflin, Evan Siemann, and Eric Vanderwerf. David Westneat kindly shared some observations on reactions to natural predators. Mike Clark, Shai Mitra, David O'Neill and Evan Siemann were very helpful with various of the data analyses. Karen Wright, Louise Gunn and Linda Harrington provided invaluable assistance in the preparation of the manuscript and Eric Klopfer helped with the figures. Bob Johnson made work at the experimental ponds pleasant and productive. I have discussed this work with a large number of colleagues, including seminar groups at Cornell, Queen's, Yale, Indiana and Princeton Universities. Particularly helpful have been discussions with Peter Dunn, Steve Emlen, Kern Reeve, Paul Sherman, and Steve Zack. Steve Emlen, David Haskell, John McCarty, Amy McCune, Bob Montgomerie, Paul Sherman, and an anonymous reviewer provided valuable input on various drafts of the manuscript.

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