

VARIATION IN SONG SPARROW NEST DEFENSE: INDIVIDUAL CONSISTENCY AND RELATIONSHIP TO NEST SUCCESS¹

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Abstract. I studied nest defense in 53 female Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia, between 1994 and 1995. A total of 75 trials was conducted by presenting a Northwestern Crow (*Corvus caurinus*) and a Dark-eyed Junco (*Junco hyemalis*) mount near nests during incubation. Female Song Sparrows spent more time perched close to the crow than the junco mount, and alarm called more often in the presence of the crow. Female responses were unrelated to their age and were not correlated with the subsequent success of their nests. Individual female responses to the junco, but not the crow mount, in 1994 were significantly positively correlated with their responses in 1995. Individual responses to a predator model may not be consistent from year to year because of experiences with live predators or the inherent variability of nest defense behavior.

Key words: Song Sparrow, *Melospiza melodia*, nest defense, nest success, female age.

INTRODUCTION

Most studies of nest defense in birds have focused on tests of parental investment theory (review in Montgomerie and Weatherhead 1988), or on providing evidence of recognition of threats to the nest (Smith et al. 1984, Bazin and Sealy 1993). Such studies assume that parents engage in defense because they receive some survival or reproductive benefit. However, the few studies on passerines designed to investigate relationships between nest defense and nest success found inconsistent patterns (Table 1). Most of these studies were conducted on unmarked populations, where individual attributes that might affect nest defense and success could not always be accounted for. In addition, most of these studies tested nest defense within one breeding season, but if defense is related to overall nesting success, then individuals should consistently be successful in defending their nests across years. This study used a population of individually-marked birds to determine if parental responses were related to nest success and if the responses of individuals were repeatable across years.

Highly variable individual responses to predator models are common in nest defense studies (Curio 1975, Regelman and Curio 1983, Hobson et al. 1988). This variation may be due to

birds with poorly concealed nests responding more strongly than those with well concealed nests (McLean et al. 1986, Hobson et al. 1988), or older birds responding more strongly than young birds due to experience with a predator (Smith et al. 1984). Older birds also may invest more than younger birds in the defense of their nests if older birds have a higher mortality rate (Montgomerie and Weatherhead 1988).

I studied a color-marked population of Song Sparrows where the breeding histories and ages of all individuals were known. Thus I was able to determine if age affected defense behavior, if individual responses were consistent across breeding seasons, and if the strength of responses to the predator mount were correlated with the avoidance of nest predation.

METHODS

I studied nest defense in Song Sparrows on Mandarte Island, British Columbia, from April-June in 1994 and 1995. Details of the Song Sparrow population, their habitat and the general study methods are given by Smith (1981) and Arcese et al. (1992). Most nests were discovered in early incubation by observing the behavior of females. Once nests were found, they were monitored every 5 days for hatching or failure. Nestlings were banded at approximately 6 days of age and nests were checked 11 days after hatching to determine if the young had fledged. I considered nesting attempts to be successful when at least one young fledged.

Concealment of the nest was estimated at day 11 or upon discovering that the nest had failed.

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TABLE 1. Studies of nest defense in relation to nesting success. Papers are grouped by defense variables that were correlated with success. Nest predators were determined from the papers themselves or the literature they cited.

Defense variable	Species	Size/Mass ^b	Nest predators	Model	Comments	Authors
Aggression	Fieldfare (<i>Turdus pilaris</i>)	25.5 cm/104 g	Crows, magpies, jays, woodpeckers, squirrels, small mustelids	Human	Colonial nesters	Andersson et al. 1980
	Eastern Kingbird (<i>Tyrannus tyrannus</i>)	22 cm/43.6 g	Crows	Human	Highly aggressive species	Blancher and Robertson 1982
	Northern Mockingbird (<i>Mimus polyglottus</i>)	25 cm/48.5 g	Crows, jays, grey squirrels, raccoons, cats, dogs ^c	Human	Highly aggressive species	Breitwisch 1988
Call rates	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	22 cm/41.5 g	Crows minks, raccoons	Human	Nests with extra-pair young included	Weatherhead 1990
	Stonechat (<i>Saxicola torquata</i>)	13 cm/15.3 g	Magpies, cats, grass snakes	Human		Greig-Smith 1980
	American Goldfinch (<i>Carduelis tristis</i>)	13 cm/12.6 g	Jays	Human, jay, American Kestrel	Calls attract conspecifics	Knight and Temple 1986a
	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	22 cm/41.5 g	Crows, minks, raccoons	Red-tailed Hawk, crow, raccoon		Knight and Temple 1988
No variables	Song Sparrow (<i>Melospiza melodia</i>)	16 cm/20.5 g	Crows, deer mice, cowbirds	Crow		This study
	Yellow Warbler (<i>Dendroica petechia</i>)	13 cm/9.2 g	Red squirrel	Grey squirrel		Hobson et al. 1988
	American Robin (<i>Turdus migratorius</i>)	25 cm/77.3 g	Crows, ravens, raccoons, Douglas squirrels	Human		McLean et al. 1986
	Willow Tit (<i>Parus montanus</i>)	11.5 cm/12 g	Great Spotted Woodpecker, red squirrel	Stoat	Intensity of defense did not differ between broods that produced recruits and those that did not	Rytönen et al. 1995
	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	22 cm/41.5 g	Crows, minks, raccoons	Human	Used only nests with young sired by the defending male	Weatherhead and Boag 1995

^a National Geographic Society, 1987. *Field Guide to the Birds of North America*. National Geographic Society, New York; or Peterson, R., G. Mounfort, and F.A.D. Hollom. 1985. *Die Vögel Europas*. Paul Parey, Hamburg, Germany.

^b Dunning, J. B. 1993. *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton, FL.

^c Personal communication.

I estimated concealment by the proportion of the nest cup that was visible (0, 25, 50, 75, 100%) from directly above and from 1 m to the side from which I first approached the nest. Well-concealed nests had no more than 25% of the nest cup visible from above and the side, whereas the visible proportion of the cup of poorly concealed nests was more than 50%.

I assessed nest defense behavior of Song Sparrows during incubation using mounts of a Northwestern Crow (*Corvus caurinus*) and a Dark-eyed Junco (*Junco hyemalis*). Each bird was mounted in a perched position with its wings folded. Northwestern Crows are one of three regular nest predators on Mandarte Island, and the junco was used as a control in this experiment as in an earlier study of nest defense in Song Sparrows on Mandarte Island (Smith et al. 1984).

A trial involved placing a 1-m tall stake, 0.5 m from an active nest at least 1 hr before presentation of a mount. Mounts were placed directly in shrubs in four cases when the height of the nest exceeded the top of the height of the stake. Mounts were put on the stake facing the nest after females left to feed. Females typically spend 7–15 min off their nests while feeding between incubation bouts (Arcese and Smith 1988; pers. observ.). I began recording female behavior when females returned to within 5 m of their nest. In seven cases where I did not observe the female returning or responding within 15 min of presenting the mount, I recorded the session as no response observed, and omitted these trials from all analyses.

Both the crow and junco mounts were presented to each female, with the order of presentation chosen at random for the first female of each age class to be tested in 1994; the order of presentation was alternated thereafter. In 1995, females first tested in 1994 were presented with the mounts in opposite order to their 1994 presentation. No significant effect of presentation order was detected in eight comparisons except for time spent incubating in the presence of the junco mount in 1995 (Mann-Whitney *U*-test, $U = 59$, $n = 31$, $P = 0.01$).

Following Smith et al. (1984), I recorded the female's distance to the mount (< 2 m, 2–5 m, > 5 m) and activity (alarm calling, flights, perching, incubating, dives/hits or out of sight) at each 10-sec interval during a 5-min trial. No flights or dives/hits were observed. "Out of sight" was recorded when the female was not

visible to the observer; the female may or may not have been out of sight of the mount. Mounts were removed immediately after each trial to allow females to incubate. The second mount was placed on the stake when the female left on her next feeding trip off the nest, usually 20–30 min later. I made observations from a ladder placed between 8 and 20 meters from the nest. Song Sparrows are relatively tame on Mandarte Island and did not appear to respond to me at these distances. There also were no statistically significant correlations between observation distance and any of the response variables ($r_s = -0.096$ to 0.171 , $P > 0.05$ for all tests).

Forty-three of 52 females that bred in 1994, and 32 of 41 that bred in 1995 were presented with mounts. I did not record responses of males because they were present in less than half of the trials and females usually responded first. I excluded four trials where males were first to respond. One female that was flushed from the shrubs by a Glaucous-winged Gull (*Larus glaucescens*) mid-trial also was excluded from analyses. Nineteen of the females presented with mounts were tested in both years. Each female was tested only once in a breeding season, either on her first or second nesting attempt. Trials were conducted between 08:30 and 19:30 PST. Trials conducted in the morning (08:30–12:00), afternoon (12:00–17:00) and evening (17:00–19:30) were not statistically different for any of the response variables (Kruskal-Wallis ANOVA, $H \leq 2.9$, $n = 18, 38, 18$, $P > 0.2$ for all comparisons).

The number of 10-sec intervals that females spent < 2 m, alarm calling, incubating and out of sight were totaled and compared using non-parametric statistical tests with SYSTAT (SYSTAT 1992). Years of the study were analyzed separately to avoid counting the same females twice. In order to calculate the power of the Mann-Whitney *U*-tests of differences in response between successful and unsuccessful females, I used SAS (SAS Institute 1995) to run 1,000 simulations of a randomly generated data set, with the same mean and variance as my own (Thomas and Juanes 1996). I report power as the percent of the 1,000 simulations that yielded a *P*-value ≤ 0.05 .

RESULTS

FEMALE RESPONSE AND AGE

Females spent more time close to the crow than the junco, and they were less likely to incubate

TABLE 2. Responses of female Song Sparrows to crow and junco mounts in terms of the number (mean \pm SE) of 10-sec intervals in a 5-min trial (total = 30 intervals) during which the activity occurred.

Response variable	Crow mount	Junco mount	P-value ^a
1994			
Less than 2 m from mount	9.1 \pm 1.4	3.8 \pm 0.8	0.001
Alarm calling	11.2 \pm 1.7	0.0 \pm 0.0	<0.001
Incubating	0.8 \pm 0.8	9.5 \pm 2.0	0.001
Out of sight	13.9 \pm 1.5	14.3 \pm 2.1	0.67
n	37	38	
1995			
Less than 2 m from mount	9.9 \pm 1.7	3.2 \pm 0.7	0.001
Alarm calling	9.7 \pm 2.1	0.0 \pm 0.0	0.001
Incubating	1.9 \pm 1.3	17.4 \pm 2.4	0.001
Out of sight	11.8 \pm 1.7	7.9 \pm 2.1	0.06
n	28	27	

^a Wilcoxon signed rank test.

in the presence of the crow (Table 2). Females also alarm called in the presence of the crow, whereas no female alarm called in the presence of the junco in either year. These responses were unrelated to age (Fig. 1). In addition, of the 19 females tested in both years, eight (42%) alarm called more often and 10 (53%) spent more time perched close to the crow when they were one year older, but a similar number of females ($n = 9$) decreased their response from one year to the next (Sign test, $P > 0.4$ for both variables).

DEFENSE AND NEST SUCCESS

Female responses were unrelated to the subsequent success or failure of nests. In 1994, females whose nests were depredated ($n = 12$) spent similar amounts of time alarm calling (Mann-Whitney U -test, $U = 186$, $P > 0.7$) and perched < 2 m ($U = 205$, $P > 0.3$) from the crow mount as females that successfully fledged young ($n = 29$). The power of these tests was 7% for alarm calling and 78% for distance. There also was no correlation between the proportion of all nests of a particular female that were successful within a breeding season and the amount of time the female spent close to the crow ($r_s = -0.021$, $n = 41$, $P > 0.5$) or alarm calling ($r_s = -0.202$, $n = 41$, $P > 0.1$). I did not attempt to relate nest success with female defense behavior in 1995 because only one nest at which the mounts were presented was depredated.

REPEATABILITY OF RESPONSE

Despite the similarity of mean responses between years (Table 2), individual female re-

sponses to the crow mount in 1994 were not correlated with their responses to the same mount in 1995. In contrast, responses to the junco mount were positively correlated across years (Table 3). The lack of statistically significant correlations between years for the crow mount may be due to the fact that females were tested on only their first nesting attempt in 1995, but were tested on either their first or second attempt in 1994. However, there was no difference in response between females tested on their first attempt and those tested on their second attempt in 1994 (Mann-Whitney U -test, $U \leq 207$, $n = 41$, $P > 0.1$ for all tests). Furthermore, limiting the correlation to females tested only during their first attempt in both years does not change the significance of the results ($n = 11$, $P > 0.05$ for all comparisons).

Variable responses between years also might reflect annual differences in nest concealment. However, there were no significant differences in response between females with well-concealed, intermediate, or poorly-concealed nests in any of the response variables considered (Kruskal-Wallis ANOVA, $H \leq 2.3$, 1994, $n = 36$; 1995, $n = 23$; $P > 0.05$, for all tests).

DISCUSSION

RESPONSE BY SONG SPARROWS

Most female Song Sparrows responded to a crow mount (potential "predator") near their nest by alarm calling and perching within 2 m of the crow. In contrast, female Song Sparrows responded to the "safe" junco mount by incubating with no alarm calling. The response to

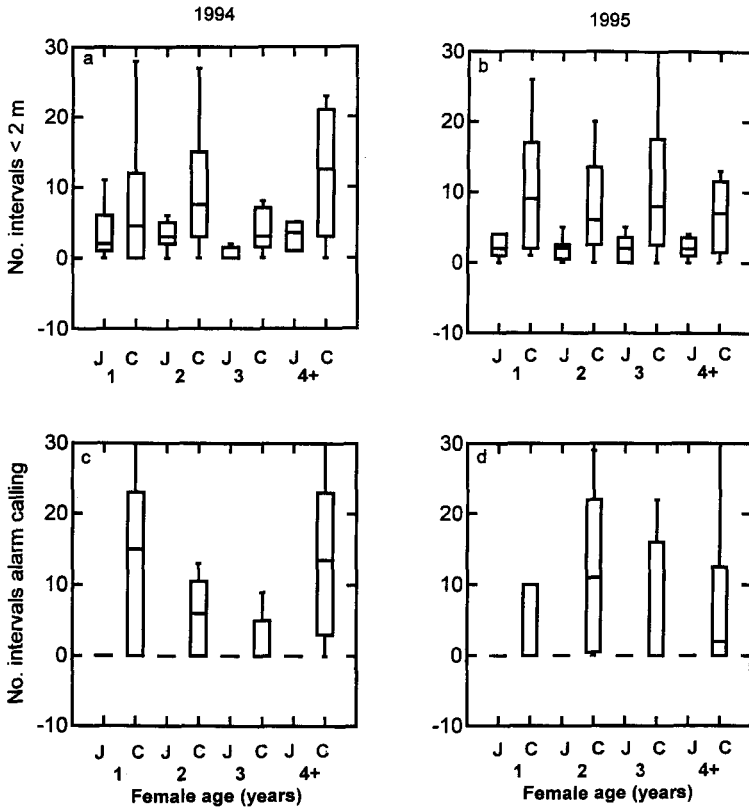


FIGURE 1. Box plots of female responses to the junco (J) and crow (C) mount in terms of the number of 10-sec intervals in a 5-min trial (total = 30 intervals) that females were perched at a distance of < 2 m from the mount (a, b) or alarm-calling (c, d). Responses are grouped by female age (1994: *n* = 18, 12, 7, 6, respectively; 1995: *n* = 5, 12, 8, 7, respectively). The box represents the interquartile range with the center horizontal line representing the median. There were no significant differences between responses among age classes (Kruskal Wallis ANOVA, all *P*-values > 0.1).

the junco was similar to that obtained with the same mount in a prior study (Table 1 in Smith et. al. 1984), and the response to the crow was similar to the descriptions of the behavior of Song Sparrows in Ontario responding to a hu-

man approaching the nest (Weatherhead 1989). Nice (1943) observed “distraction displays” by Song Sparrows in Ohio, as well as “threats” and “attacks” when she or potential nest predators approached a nest. She observed threats only when young were present. I may not have observed the full range of defensive behaviors because I tested all females during incubation. Nevertheless, the stronger response of Song Sparrows to the crow rather than the junco suggests that females recognized crows as a potential threat to their nests on Mandarte Island.

TABLE 3. Spearman rank correlations (between 1994 and 1995) of female responses to each mount.

Response variable	Crow mount (<i>n</i> = 19)	Junco mount (<i>n</i> = 18)
Less than 2 m from mount	-0.36	0.50*
Alarm calling	0.14	N/A ^b
Incubating	N/A ^a	0.46*
Out of sight	0.16	0.53*

^a Too few females incubated in the presence of the crow to have a meaningful sample size.

^b No female alarm called at the junco, thus there are no values to correlate.

* *P* ≤ 0.05.

FEMALE AGE

Older birds are predicted to respond more strongly to a threat to the nest than younger birds, if older birds are less likely to survive to breed in the next season (Montgomery and

Weatherhead 1988). However, if survival is independent of age, one would not expect older birds to invest more heavily than younger birds in their current reproduction (Weatherhead 1989). I found that older female Song Sparrows did not spend more time close to the mounts or alarm calling than younger females. Weatherhead (1989) also found that older male Song Sparrows did not consistently differ in nest defense from when they were tested at a younger age. Both results are consistent with the fact that survival of adult Song Sparrows generally is independent of age (Nol and Smith 1987). Most other studies of passerines also have not found significant relationships between age and nest defense (Curio 1975, Breitwisch 1988, Hobson et al. 1988, Winkler 1992).

Older birds also might be expected to respond differently than younger birds to a predator at the nest because older birds have gained experience or knowledge of a predator as a threat. Smith et al. (1984) found that adult female Song Sparrows responded more strongly to a mounted female Brown-headed Cowbird (*Molothrus ater*) than did yearlings, and they demonstrated that the increase in response resulted from females acquiring experience with cowbirds late in their first or second breeding season. Yearling and adult female Song Sparrows may respond strongly and similarly to Northwestern Crows because the crows are resident on Mandarte Island, providing the opportunity for Song Sparrows to learn to recognize them as threats early in life. Alternatively, Song Sparrows may recognize crows as enemies innately, as do some other passerines presented with nest predators (Curio 1975, Hobson et al. 1988).

CONSISTENCY OF RESPONSES

Female Song Sparrows on Mandarte Island consistently responded more strongly when presented with a crow mount versus a junco mount at their nests. However, the responses of individual females to the crow mount in one year were not significantly correlated with their responses in the next year. Curio (1975) found significant correlations in response strength for individual Pied Flycatchers (*Ficedula hypoleuca*) between breeding seasons, despite observing large variation in response strength. McLean et al. (1986) and Winkler (1992) also found that defending birds responded consistently on at least some variables when they were re-tested within a sin-

gle nesting attempt. However, McLean et al. found no correlation in defense response between nesting attempts.

One possibility for the lack of significant correlation between years for the crow mount is that conditions were not sufficiently similar for all individuals between years. Many factors have been shown to be correlated with nest defense behavior, including brood size (Robertson and Biermann 1979, Knight and Temple 1986a), time of season (Barash 1975, Regelman and Curio 1983, Curio et al. 1984), and nest concealment (McLean et al. 1986, Hobson et al. 1988). I attempted to account for some of these factors by conducting tests early in the season during the incubation period when responses have been found by others to be relatively consistent (Greig-Smith 1980, Breitwisch 1988, Weatherhead 1989). I also found no significant relationships between nest concealment and response, and all females tested had clutches of similar size (3–4 eggs). Nevertheless, it is possible that factors I did not measure, such as predator density or motivation of the parents, changed between years and affected nest defense.

Another reason for the lack of significant correlation of individual responses to the crow mount may be that females' responses were modified by the model presentations or encounters with actual predators. Knight and Temple (1986b) suggested that birds might increase their response with repeated "successful" encounters with the same predator model. However, females in my study were tested only once in each year, and only half of the females increased their responses from one year to the next. Rytönen and Soppela (1995) present four hypotheses about how experiences with predators might modify parental responses, three of which predict an increased response with experience. Although these authors were able to infer the amount of exposure birds had to one avian predator, without constant observation or captive conditions, it would be difficult to determine the number and nature of encounters with real predators.

NEST SUCCESS

Most nest defense studies assume birds respond to a model nest-predator in a similar manner as they would to a real predator, and that birds respond to nest predators because the benefits of doing so outweigh the costs of defense. I was

unable to find an association between nest defense and the success of nests in Song Sparrows on Mandarte Island. This may have occurred because nest defense was generally ineffective, or because other factors such as nest placement and territory quality play a much larger role in determining the outcome of a nesting attempt. However, if nest defense was completely ineffective, it would be difficult to explain why birds respond at all, or why they respond differently to known predators versus controls.

It is possible that successful females respond differently than unsuccessful females, but I was unable to detect this difference with my methods and sample sizes. The power of the Mann-Whitney *U*-test of differences in the number of intervals spent close to the mount was relatively high, but it was very low for the number of intervals spent alarm calling. The low power for alarm calling is attributable to the small difference between successful and unsuccessful nests in time spent alarm calling (0.13 intervals). I would have needed an impossibly large sample size to detect a difference this small with the large amount of variation in this response, and it is doubtful that a difference of less than one 10-sec interval of alarm calling is biologically meaningful.

I used only one predator model, a Northwestern Crow, to measure the nest defense response of Song Sparrows. Female responses to crows may not resemble their response to other predators which may be responsible for the majority of nest predation events. Deer mice (*Peromyscus maniculatus*) and Brown-headed Cowbirds also are probably nest predators on Mandarte Island (Arcese et al. 1992, 1996). Mean responses of adult female Song Sparrows to a mounted cowbird in a previous study (Table 1 in Smith et al. 1984: < 2 m: 21.4; Alarm: 16.9) were slightly higher than the responses I observed for a mounted crow (Table 2). Deer mice may depredate nests at night when Song Sparrows are potentially less able to defend their nests, but we know little about interactions between these two species.

Of 11 other studies of passerine nest defense that have considered the efficacy of defense, three found no correlation between response and nest success and one found no correlation between defense and the number of recruits to the breeding population (Table 1). There are no similarities between these studies and my own in

terms of type of predator, size of the bird or type of mount used, that readily account for the lack of relationship between nest defense and nest success. However, studies that found nest defense and nest success to be positively related tended to be those conducted on highly aggressive species, such as the Eastern Kingbird (Blancher and Robertson 1982), or on those species that mob predators in groups (e.g., Knight and Temple 1986a). One easily can imagine that individual aggressiveness and/or the ability to recruit conspecifics and other species to mob predators by alarm calling would be related to success in driving predators away (Greig-Smith 1980, Knight and Temple 1986a, 1988).

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