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Nest-site selection in Savannah sparrows: using gulls as scarecrows?

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Abstract. Savannah sparrows, *Passerculus sandwichensis*, breeding on Kent Island, New Brunswick, Canada, have two types of nest predators, one of them (herring gulls, *Larus argentatus*) abundant but relatively ineffective, the other (American crows, *Corvus brachyrhynchos*) scarce but highly effective. We hypothesized that the net effect for Savannah sparrows of nesting near gulls would be to reduce the overall risk of nest predation. Despite being surrounded by predators, the eggs and offspring of sparrows that nested among gulls survived as well during the incubation and post-fledging periods as did those of sparrows that did not nest among gulls. During the nestling period, sparrows nesting among gulls had significantly lower predation rates. In defending their own nests from predatory crows, gulls apparently shielded nearby sparrows from the more dangerous predator. Experiments with model predators demonstrated that sparrows reacted to gulls as potential predators of their eggs and nestlings. Sparrows apparently recognized crows as a far greater threat, however. The tendency to nest near gulls appeared not to be heritable or influenced by early experience. Sparrows nesting among gulls were indistinguishable from sparrows nesting away from gulls in terms of body size, age and date of nesting. By choosing nest sites in microhabitats that gulls avoided, such as dense patches of goldenrod and blueberry, and by adopting more cautious approaches to their nests, sparrows nesting near gulls reduced their risk of predation by gulls. The density of Savannah sparrow nests was inversely correlated with the density of gull nests, which suggests that sparrows avoided gulls despite the apparent advantage in terms of reduced nest predation by crows. A strong nesting association between gulls and birds like Savannah sparrows is unlikely to evolve because of the low heritability of the trait, gene flow from other populations where avoiding gulls and other potential predators is selectively advantageous, and constraints on short-lived birds in learning to differentiate situations in which a predator presents a threat from those in which it provides protection.

Birds often locate their nests near predators despite what seem to be substantial risks to themselves or to their offspring. Researchers have offered two explanations for why birds nest near predators. The first assumes that nesting near predators is risky but emphasizes that birds are constrained in acquiring safer nest sites. Even though nesting near predators may reduce reproductive success compared with nesting elsewhere, birds that are young, ageing, ailing or socially subordinate may have few other options (Blus & Keahey 1978; Reese & Kadlec 1985; Lessels & Krebs 1989). Species with specialized nesting requirements, such as birds that must breed on islands that happen to be inhabited by predators, may face similar limitations (Bourget 1973). Nest associations with predators may also be an incidental consequence of shared habitat preferences (Erwin et al. 1981). Inexperienced birds may unintentionally nest near predators because they fail to recognize the dangers (Wheelwright & Schultz 1994). Finally, nest-site selection may not be as flexible a trait as is often presumed if nesting behaviour is learned at a young age or has a genetic basis. In other words, birds raised near predators may nest near predators because of their early experience or genes.

An alternative explanation for nesting near predators is that the benefits outweigh the greater

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risks of predation. In theory, the increased risk of egg or nestling loss incurred by nesting near predators could be compensated by improved adult survival or reduced competition for food. In certain cases, one predator may actually provide protection against another, more effective predator. For example, common eiders, *Somateria mollissima*, nesting within gull (*Larus* spp.) colonies experience lower rates of nest predation than eiders nesting elsewhere, even though gulls sometimes eat eider eggs and chicks, because gulls also alert against or drive off more dangerous predators such as bald eagles, *Haliaeetus leucocephalus*, or minks, *Mustela vison* (Bourget 1973; Gerell 1985; Götmark & Åhlund 1986; N.T. Wheelwright, personal observation; see also Dwernychuk & Boag 1972). Likewise, grebes (*Podiceps occipitalis*, *Rollandia rolland*) nesting in association with brown-headed gulls, *L. maculipennis*, may lose their nests to gulls (Burger 1984). They have higher reproductive success and lower adult mortality than grebes nesting outside gull colonies, however, because, forewarned by the gulls about the approach of predators, the grebes can adopt appropriate anti-predator behaviours. Spotted sandpipers, *Actitis macularia*, nesting within common tern, *Sterna hirundo*, colonies experience more predation by migratory ruddy turnstones, *Arenaria interpres*, than do sandpipers nesting outside tern colonies, but experience less predation by minks, which pose the larger threat to sandpipers (Alberico et al. 1991). Birds nesting near colonies of biting ants or stinging wasps may gain protection against predatory snakes and primates (Young et al. 1990; Joyce 1993). A prerequisite for using one predator as protection against another is the ability to distinguish between different predators and to assess the relative danger presented by each, which is known in a variety of bird species (Nice & ter Pelkwyk 1941; Curio 1975; Walters 1990; Winkler 1992).

Although protective nest associations between bird species have long been documented, and plausible hypotheses have been advanced to explain them as adaptations (Koskimies 1957; Cullen 1960; Kruuk 1964; Drycz et al. 1981), few studies have been able to discriminate between the ‘constraint’ and ‘benefit’ hypotheses, because the fitness consequences (e.g. lifetime reproductive success, offspring recruitment) of nesting near versus far from predators are notoriously difficult to measure completely, information about a bird’s early experience and the heritability of nesting behaviour is generally lacking, and studies have been relatively short-term or non-experimental (but see Nuechterlein 1981). We were able to avoid some of these shortcomings by taking advantage of a marked, known-age bird population in which reproductive success and the heritability of behaviour could be estimated over an 8-year period.

To evaluate possible advantages and disadvantages of nesting near predators, we compared the behaviour and reproductive success of Savannah sparrows, *Passerculus sandwichensis*, nesting in the presence and absence of herring gulls, *L. argentatus.* Although gulls prey on Savannah sparrows and their offspring (Wheelwright & Rising 1993), we hypothesized that for Savannah sparrows the net effect of the presence of gulls would be to reduce the overall risk of nest predation, because the gulls ward off more effective predators, American crows, *Corvus brachyrhynchos.* We attempted to distinguish between the constraint hypothesis and the benefit hypothesis by (1) quantifying the relationship between nest-site selection and fledging success, fledgling size, offspring-recruitment rate and adult survivorship; (2) determining whether the decision to nest among predators was related to a bird’s sex, body size, age, parentage or experience as a nestling; (3) assessing how birds nesting among predators might change their behaviour patterns to reduce their risk of predation; (4) testing whether the behaviour patterns of birds towards different predators were gauged in some measure to the threats posed by the predators. We also examined seasonal variation in predation risk and compared the responses of Savannah sparrows to model predators presented at different stages of reproduction (Patterson et al. 1980; Knight & Temple 1986).

Hypotheses

Our first hypothesis was that sparrows would recognize both gulls and crows as potential nest predators and would distinguish them from similar-sized animals that posed no threat to eggs or nestlings. We also expected the intensity of the sparrows’ responses to reflect the magnitude of the perceived danger to their offspring. Thus, sparrows should demonstrate greater alarm in response to the presence of a crow near their nest than to the presence of a gull, because crows were observed to be more systematic and effective nest predators. Second, we predicted that the reproductive success of Savannah sparrows nesting near gulls would be as high as or higher than that of sparrows nesting away from gulls because, although gulls prey opportunistically on sparrow nests, they also tend to chase away crows, the more dangerous predator. Assuming that the first two hypotheses were supported, our third hypothesis was that Savannah sparrows would choose the lesser of two evils and preferentially nest in areas of high gull density.

METHODS

Study Site

Our study site was on Kent Island, an isolated 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35′ N, 66°46′ W). The study was centred in two open fields where Savannah sparrows nest at high densities. The South Field site is a 6-ha portion of an extensive open habitat which supports a large breeding colony of herring gulls (Cannell & Maddox 1983). The North Field is a 1.3-ha field surrounded by white spruce, *Picea glauca*, located several hundred metres from the South Field. The fields are divided by mowed paths into 43 quadrats of 0.25-ha (50 × 50 m). Approximately one-third of the Kent Island Savannah sparrow population breeds in the South and North Field study area (Dixon 1978; N. T. Wheelwright, personal observation).

Study Species

On Kent Island, Savannah sparrows (hereafter sparrows) establish territories in coastal vegetation, marshes, low woody vegetation and open fields. By 1 year of age, both male and female sparrows are reproductively mature. Their nests, which are built directly on the ground by the female, are exceedingly well concealed, typically covered by vegetation and accessible only by a narrow grass-lined tunnel (Wheelwright & Rising 1993). By the time the sparrows return from their southern wintering grounds in early May, gulls are already present and preparing to nest, so the density of gulls within a sparrow's prospective territory can be easily assessed early in the season. Female sparrows appear to be relatively free to choose nest sites in different habitats. Breeding dispersal by males and females is negligible, however; once a female nests in a particular location, she generally locates future nests near her original site regardless of the density of sparrows or gulls (N. T. Wheelwright & R. A. Mauck, unpublished data).

Each summer from 1987 to 1994, all Savannah sparrows in the South and North Fields were banded with U.S. Fish and Wildlife Service aluminium bands and a unique, randomly determined combination of three plastic colour bands. During daily censuses, the sparrows' behaviour patterns (singing, foraging, mate guarding, feeding nestlings or fledglings) were recorded on field maps (scale 1:1200). All but a few sparrow nests within the study area were located each year (Wheelwright & Schultz 1994). Nest sites were designated with 6.3 × 8.8-cm vinyl flags on wire stakes placed 3 m south of the nest itself; we inconspicuously bent several blades of dry grass or goldenrod (*Solidago* spp.) stems directly over the nest to help us relocate it. As a precaution against predators learning to associate flags with nests, we placed dummy flags throughout the study area. We found no difference in predation rate between marked and unmarked nests (chi-square test: $P>0.50$; $N=16$ nests). Nests were checked every other day until the first nestlings hatched and then not again until the nestlings were 7 days old (2 days before fledging), whereupon the nestlings were measured and banded. With no mammalian predators on Kent Island, the frequency of our nest visits probably did not appreciably increase predation risks (Major 1990; N. T. Wheelwright, unpublished data). We also recorded the fate of each nest (fledged successfully, abandoned or preyed upon during incubation or the nestling period).

Herring gulls and American crows are by far the most important predators of Savannah sparrow eggs, nestlings and fledglings on Kent Island. They are two of the most abundant species of predators on the island, with population sizes of about 9000 (Cannell & Maddox 1983) and 50 (N. T. Wheelwright, personal observation), respectively, and both species readily eat sparrows at all stages of development (based on direct observations and the discovery of fledgling and, infrequently, adult sparrow bands in herring gull pellets; see also Dixon 1978). Greater black-backed gulls, *L. marinus*, and common ravens, *C. corax*, nest on Kent Island and may opportunistically prey on the eggs and nestlings of small birds, but they are much less common than their congenors (about 40 and 8 individuals, respectively). Other potential avian predators of Savannah sparrows occur on Kent Island only during migration. No reptiles have been found on the island, and none of the island's few mammal species (snowshoe hares, *Lepus americanus*, muskrats, *Ondatra zibethica*, and bats, *Myotis* spp.) preys on nests.

Observations of the foraging behaviour of herring gulls (hereafter gulls) and crows suggested that crows pose a greater threat to sparrows even though gulls are much more common within the study area. Gulls spend much of the day near their nests, guarding or incubating their own eggs (Pierotti & Annett 1991) or interacting with other gulls rather than hunting for the eggs of other species (Pierotti 1983). Most of their foraging is done in the inter-tidal zone or at sea, although they sometimes hunt in the fields for insects. Gulls apparently only prey on the cryptic Savannah sparrow nests when they happen upon them in their search for insects or incidentally flush the incubating female (cf. Vickery et al. 1992). Sparrow nests within 1 m of active gull nests routinely fledged young, despite the fact that parent sparrows made more than 200 conspicuous feeding trips per day during the nestling period (Wheelwright et al. 1992). Crows, on the other hand, typically forage methodically in small groups which sweep through the fields. Crows are also proficient at remembering the locations of individual nests (Sonerud & Fjeld 1987). Both gulls and crows avoid walking through dense patches of goldenrod and raspberry, *Rubus idaeus*, but crows (unlike gulls) habitually fly between lowbush blueberry patches, *Vaccinium angustifolium*, a popular nesting habitat of Savannah sparrows, and land on them in a systematic search for nests (see also Sullivan & Dinsmore 1990). In the cases where we have watched crows hunt for nests and eat sparrow eggs or nestlings, they appeared to cue in on sparrow alarm calls, narrowing their search as the intensity of alarms increased (N. T. Wheelwright & J. Mitchell, unpublished data). Crows will also steal eggs from gull nests (Ewins 1991; N. T. Wheelwright, personal observation), which presumably explains why gulls attack crows near their nests and why we rarely noticed crows foraging in the immediate vicinity of nesting gulls.

Between 1987 and 1994, Savannah sparrows nested at a mean ± SD density of 6.2 ± 6.1 females/ha in the study site. Densities varied between quadrats, however, with 0–32 females nesting per quadrat (ANOVA; $P<0.006$; $N=43$ quadrats). Herring gulls nested at a mean density of 17.4 ± 33.5 pairs/ha within the study area. The density of gull nests varied between quadrats but not between years (ANOVA; between quadrats: $P<0.0001$; between years: $P=0.86$). Therefore, we calculated mean gull nest densities for each quadrat and assigned each quadrat to one of four categories of gull density: (1) zero ($\bar{X}\pm$ SD number of gull pairs/ha$=0\pm0$, $N=21$ quadrats); (2) low (2.8 ± 2.2, $N=7$); (3) intermediate (7.7 ± 7.2, $N=6$); (4) high (67.9 ± 30.7, $N=9$; for certain analyses, we combined zero plus low density quadrats, and intermediate plus high density quadrats). Both the South and North Fields were dominated by a few species of grasses and herbaceous plants, with scattered patches of lowbush blueberry, raspberry and blackberry, *Rubus* spp., and rough goldenrod, *S. rugosa.* Vegetational features bore little relationship to gull density (McCain 1975; N. T. Wheelwright & P. Hodum, unpublished data) and the entire study area was suitable as both sparrow- and gull-nesting habitat. Most (but not all) quadrats with intermediate or high gull densities tended to occur within 100 m of the shore, but none of the quadrats within the study area was further than 200 m from the shore. Because gulls and crows did not nest in the North Field and only rarely hunted there, we separately analysed Savannah sparrow nest densities and reproductive success in the two areas.

In 1988 we quantified the feeding behaviour of sparrows during 30 1-h observations at seven nests located in areas of zero–low gull densities and 29 1-h observations at seven nests in areas of intermediate–high gull densities. We recorded the number of visits/h by females and the amount of time they spent on perches before entering the nest, using 10 × binoculars at 30–50 m. In 1995, we observed nest-hunting behaviour by crows as part of a separate study of corvids.

Procedures

We conducted a series of experiments using artificial sparrow nests and model predators. We placed Savannah sparrow nests, each containing four eggs, near gull nests to monitor egg disappearance rates in early June 1991. The nests and eggs (of tree swallows) had been saved from a separate study on age-related reproduction (Wheelwright & Schultz 1994); tree swallow eggs are similar in size to those of Savannah sparrows, but they are pure white rather than dull brown with speckles. The sparrow nests were hidden in natural vegetation in matched pairs at distances of 1 m and 5 m from each of 10 gull nests ($N=20$ artificial nests).

To test sparrows' reactions to different predators, we presented 37 breeding female Savannah sparrows with life-size standing plastic models of herring gulls and American crows (Carry-Lite Inc., Milwaukee, Wisconsin, U.S.A.). As a control, we initially used a model flamingo, which was similar in size to both the gull and crow models. The sparrows paid little attention to it, however, so we used no model for the rest of the controls. Experiments were conducted halfway through both the incubation and nestling periods in all weather except heavy rain, as described below. Parental age, clutch size and brood size did not vary between treatments (ANOVA; $P>0.30$, $N=37$ females).

In experiments conducted during the incubation period, one of the model predators (crow or gull) was randomly selected and concealed in a bag until we placed it in a realistic position on the ground 5 m from a Savannah sparrow's nest. We made all behavioural observations using a 15× spotting scope and 10× binoculars while hidden in a blind or behind tall vegetation at least 25 m from the nest and 30 m from the model (Wheelwright et al. 1992). After the female sparrow appeared near her nest, we recorded the number of alarm calls, the length of time between her arrival and actual entrance to the nest, her method of approach (flying directly to the nest, flying to a perch within 1 m of the nest and walking the rest of the way, or walking from a distance of >1 m), the closest distance that the female approached the model, and the length of her incubation shift after she entered the nest. The time that a female actually entered her nest was estimated by extrapolating from a female's speed over the ground, noting the time when vegetation stopped moving, and listening for the cessation of soft alarm notes. If the female did not enter the nest within 30 min, the model was removed. After the incubation shift was completed and the female had left the nest, the model was removed and the same observations were made without the model present.

A similar procedure was followed during the nestling period. To avoid habituation to the models, a female that was exposed to a crow model during incubation was presented with a gull model during the nestling period, and vice versa. At each nest, we recorded the number of times that the male and female sparrow arrived carrying food, the length of time between arrival and actual entrance of the nest and the method of approach, as described above. After 30 min, the model was removed and the same observations were made without the model present.

We performed ANOVAs to determine the effect of model type (crow versus gull), time of season (early versus late clutches), the stage of reproduction (incubation versus nestling period), and location of nest-site (quadrats where gull density was zero–low versus intermediate–high) on the behavioural variables described above.

Finally, we exposed gulls to crow models placed 5 m from their nests and recorded their behaviour from at least 30 m away. The time that it took gulls to respond to the models as well as the nature of their response were recorded during the incubation and nestling periods. Except where noted otherwise, descriptive data are presented as means ± SD. Statistical analyses were performed using Statview (Abacus Concepts 1992).

RESULTS

Nest-site Selection by Savannah Sparrows

Savannah sparrows nested at higher densities in quadrats where gull density was relatively low. The density of first-clutch nests (which corresponds to the number of individual breeding females) in quadrats where gulls were absent was nearly twice that of quadrats where gull density was high, despite similarities in vegetation structure (zero gull density: 7.9 ± 7.7 sparrow nests/ha; low gull density: 6.1 ± 5.9; intermediate gull density: 5.3 ± 4.4; high gull density: 4.3 ± 4.5; one-way ANOVA; $P=0.017$). Sparrow nest density also varied between years, but the negative effect of gull density on the density of sparrow nests remained significant when controlling for year (two-way ANOVA; year: $P<0.01$; gull density:

$P=0.02$; year × gull density: $P=0.53$). The number of sparrow nests per quadrat was negatively correlated with gull density (Spearman rank correlation: $r_S = -0.42$; $P=0.02$).

We found no evidence that young, inexperienced or subordinate individuals were more likely to nest in sites with high densities of gulls. The mean ± SD age of female Savannah sparrows and their mates in different quadrats was independent of gull density (zero gull density: 1.9 ± 1.1 and 1.8 ± 1.2 years, respectively; $N=97$ pairs; low gull density: 1.9 ± 1.1 and 2.1 ± 1.5 years, $N=71$; intermediate gull density: 2.2 ± 1.1 and 1.9 ± 1.2 years, $N=57$; high gull density: 1.9 ± 1.3 and 1.8 ± 1.1 years, $N=49$; one-way ANOVA; $P>0.42$ for both sexes). Likewise, there was no relationship between gull density and various measures of body size (wing length, tarsus length, body mass, bill length, bill depth; one-way ANOVA; $P>0.10$ for all comparisons) of nesting sparrows. There was also no indication that sparrows that nested among gulls were late arrivals from spring migration faced with fewer choices of nest sites. The mean date of hatching of the first clutch in quadrats where gull densities were zero, low or high differed by only 0.3 days ($N=72$, 40 and 35 nests, respectively). The mean date of hatching in quadrats with intermediate gull densities ($N=40$ nests) was less than 2 days later than in other quadrats, and overall there was no significant relationship between gull density and date of hatching (one-way ANOVA; $P=0.51$; two-way ANOVA; year: $P=0.09$; gull density: $P=0.46$; year × gull density: $P=0.99$).

To determine whether the choice of nest sites by sparrows was influenced by early experience or a possible genetic predisposition, we examined the relationship between gull densities near an individual's natal nest and its first adult nest. Both female and male sparrows appeared to choose nest sites independently of their natal nest site, although our data suggested that males may be more likely than females to select breeding sites with gull densities similar to their natal site (Table I).

Table I. Relationship between gull density near a Savannah sparrow's natal nest and gull density near its first adult nest. For neither females nor males was there a significant relationship, although male sparrows showed a slightly greater tendency than females to nest in areas with gull densities similar to their natal nest site (chi-square test: females: $P=0.70$; males: $P=0.09$)

Gull density near adult nest	Gull density near natal nest	
	Zero–low	Intermediate–high
Females		
Zero–low	22	14
Intermediate–high	14	7
Males		
Zero–low	26	15
Intermediate–high	5	10

The behaviour patterns of sparrows nesting in areas where gulls were common were distinctive in several respects. Compared with sparrows breeding in areas where gulls were absent or scarce, sparrows nesting near gulls disproportionately selected nest sites in dense patches of lowbush blueberry and goldenrod. The vegetation surrounding their nests was about 4.5 cm taller, on average, than that of sparrows breeding in areas of low gull density. Sparrow nests in areas of intermediate–high gull density were more likely to be open rather than covered (like greater vegetation height, a consequence of placing their nests among blueberry and goldenrod).

Sparrows nesting among gulls also seemed unusually wary in approaching their nests. They tended to give more alarm calls and were often indirect in approaching their nest, flying to within 1 m of the nest and then walking the rest of the way. Sparrows nesting near gulls spent more time on nearby perches before entering the nest to feed their young. Near gulls, under natural conditions, sparrows perched for 7.1 ± 4.2 min before entering the nests, compared with 5.1 ± 4.2 min for sparrows far from gulls (ANOVA; $P=0.07$; $N=59$ 1-h observation periods). Feeding rate did not vary as a function of gull density (22.1 ± 6.0 trips/h near gulls versus 21.3 ± 2.8 trips/h away from gulls; ANOVA; $P=0.76$). One consequence of the cautious behaviour of sparrows nesting near gulls was that their cryptic nests were more difficult for us to find. In areas where gulls were absent, we found nests an average of 6.3 ± 5.0 days ($N=163$) before hatching; where gull densities were low, the interval between discovery and hatching was similar (6.4 ± 5.3 days, $N=111$). Where gulls were common, on the other hand, we sometimes did not discover nests until shortly before hatching (intermediate gull densities: 4.5 ± 5.7 days, $N=110$; high gull densities: 3.0 ± 5.7 days, $N=97$; ANOVA; $P<0.001$). Another reason that nests were hard to find was that sparrows nesting among gulls took advantage of alarm calls by gulls and frequently flushed from their nests as soon as the gulls warned of our approach (e.g. Burger 1984).

Reproductive Consequences of Nest-site Selection

To control for site effects as well as seasonal changes in vegetation height and the foraging behaviour of gulls and crows, we focused on first clutch nests in the South Field study site (we found qualitatively similar results when we repeated the analysis with the entire sample of nests). Predation rates did not differ significantly between years (ANOVA; $P > 0.10$), so we combined data from all 8 years of the study.

Of 163 nests located in quadrats where gull densities were intermediate–high, 70.7% fledged at least one young. In contrast, only 55.7% of nests fledged young in quadrats where gull densities were zero–low ($N = 103$; chi-square test; $P = 0.02$). Merely tallying up the proportion of nests that fledged young can give a biased picture of actual predation risks, however, unless all nests are monitored for the same length of time, which was not the case in our sample because of the difficulty in finding nests near gulls (see above; Mayfield 1975; Hensler & Nichols 1981). We corrected for different amounts of exposure to predators by calculating daily survival rates during the incubation and nestling periods.

There was no difference in the probability of predation during the incubation period in areas where gulls were absent or scarce compared with areas where gulls were relatively common. Daily survival rates where gull densities were zero–low averaged 0.945 ± 0.008 ($N = 167$ nests). In quadrats where gull densities were intermediate–high, daily survival rates averaged 0.934 ± 0.014 ($N = 99$ nests; $P > 0.10$ using Hensler & Nichols' (1981) Mayfield test statistic). The overall probability of survival over the entire 12-day incubation period where gull densities were zero–low was 0.504 (0.945^{12}) and 0.443 where gull densities were intermediate–high.

During the nestling period, the intensity of predation declined markedly compared with the incubation period. Nests away from gulls had significantly lower daily survival rates than those where gulls were common (zero–low gull densities: 0.972 ± 0.005, $N = 120$ nests; intermediate–high gull densities: 0.989 ± 0.004, $N = 77$ nests, $P < 0.01$; Hensler & Nichols 1981; probability of surviving the entire 10-day nestling period $= 0.750$ versus 0.898, respectively). Overall, the probability of surviving from egg laying until fledging (the product of the probabilities of surviving the incubation and nestling periods) was 0.378 in areas with zero–low gull densities, and 0.398 in intermediate–high gull densities.

Unlike the South Field study site, the North Field had neither gulls nor crows nesting near it, and neither predator foraged there often. As a result, predation on Savannah sparrow nests was relatively low in the North Field. There, daily survival rates averaged 0.989 ± 0.003 during incubation ($N = 122$ nests) and 0.995 ± 0.002 during the nestling period ($N = 111$ nests), both significantly higher than in the South Field ($P < 0.001$ and 0.03, respectively; Hensler & Nichols 1981). Survival probabilities in the North Field were 0.876 for the entire incubation period, 0.951 for the entire nestling period and 0.833 for the period from egg laying until fledging. Differences in survivorship were apparently not related to differences in food availability between the two study sites. Moreover, nestling diets (Wheelwright et al. 1992) and the mean mass of 7-day-old nestlings (2 days before fledging; Wheelwright et al. 1994) were unrelated to gull density (one-way ANOVA; $P > 0.40$).

Because Savannah sparrows nesting on Kent Island show such strong natal philopatry (N. T. Wheelwright & R. A. Mauck, unpublished data), we were able to estimate the effect of gull density on the survival of young after fledging by monitoring the return rates of yearlings that had been banded as nestlings. Sparrows that fledged from areas where gulls were absent or scarce were no more likely to return the following year than sparrows that fledged from areas where gulls were relatively common. Of 747 fledglings from South Field areas of zero–low gull density, 78 (10.4%) returned the following year, compared with 64 of 632 (10.1%) from areas of intermediate–high gull density (chi-square test; $P = 0.92$). Post-fledging survival was significantly lower in the South Field than in the virtually predator-free North Field, however, where 50 of 334 fledglings returned (15.0%; $P = 0.02$).

Without being able to take advantage of female sparrows flushing from their nests, gulls were ineffective at finding sparrow nests. No eggs were removed from any of the artificial sparrow nests after 12 days, regardless of whether the experimental nests were located 1 m or 5 m from an active gull nest. When eggs were presented in an obvious way to gulls, or if the gulls happened upon a nest, the eggs were readily consumed (N. T. Wheelwright, personal observation).

Behavioural Responses to Potential Predators

Savannah sparrows reacted to the presence of live and model predators near their nests by perching at a distance of 1–5 m from the predator and uttering alarm calls, a series of high-pitched notes at intervals of 1 s or less (Wheelwright & Rising 1993). As potential predators approached the nest, the interval between notes became shorter and the calls became louder and higher pitched. When a predator was near their nests, birds erected their crest feathers and often flew around the nest area, occasionally dropping to the ground and walking about before perching again to observe the potential predator. Males sometimes sang softly until the female entered the nest to incubate.

Responses to Model Predators

The amount of time it took female Savannah sparrows to enter the nest in the presence of a model predator did not vary as a function of the stage of the reproductive cycle (incubation versus nestling period; ANOVA; $P=0.93$, $N=146$ trials; Fig. 1). Therefore, in the following analyses, we combined trials conducted during the incubation and nestling periods. The results presented below were similar even when incubation and nestling periods were considered separately.

The lack of a difference between the incubation and nestling period indicated that the hesitance sparrows showed was related more to an avoidance of revealing their nest's location (or perhaps being caught themselves on the nest) than to defence of their offspring per se (see below). The stage of young had less influence on the responses of adult sparrows to models than the type of predator. Our experiments were not designed to test parental responses to changes in investment in or reproductive value of offspring (e.g. Gottfried 1979; Weatherhead 1979; Patterson et al. 1980; Montgomerie & Weatherhead 1988; Redondo 1989).

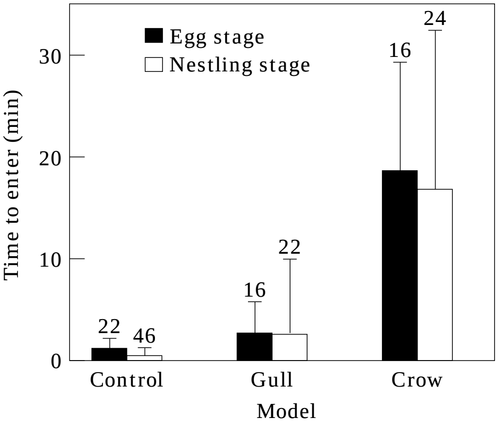

Figure 1. Mean ± SD amount of time (min) that female Savannah sparrows spent before entering their nests after detecting a model predator placed 5 m from the nest. Sparrows delayed significantly longer in the presence of a crow model than a herring gull model or control (ANOVA; $P<0.001$). Their hesitancy was independent of stage of reproduction (ANOVA; $P>0.10$). N trials given above error bars.

There was no effect of the type of predator on the number of alarm calls given by sparrows (Mann–Whitney U-test; $P=0.47$), the length of a female's incubation shift once she entered the nest (in the presence of the gull model: 21.2 ± 10.4 min; crow model: 19.3 ± 10.8 min; $P=0.50$), or the closeness of her approach to the model (minimum proximity to the gull model: 3.3 ± 1.4 m; to the crow model: 2.8 ± 1.6 m; $P=0.32$). Females delayed longer before entering their nests if a gull model was present than if no predator was present (ANOVA; $P<0.0001$; Fig. 1). Their delay was significantly greater in the presence of the crow model; they took seven times as long on average to enter the nest as when the gull model was present, and 25 times as long as when no model was present (ANOVA comparing the effect of crow models versus gull models, and crow models versus controls: $P<0.0001$; Fig. 1).

The type of model predator also significantly affected the method of nest approach by female sparrows. When no model was present, 60% of the females flew directly to the nest. When a gull model was present, only 39% made direct approaches, and when a crow model was present only 7% made direct approaches (chi-square test; $P<0.0001$; $N=146$ trials; Fig. 2).

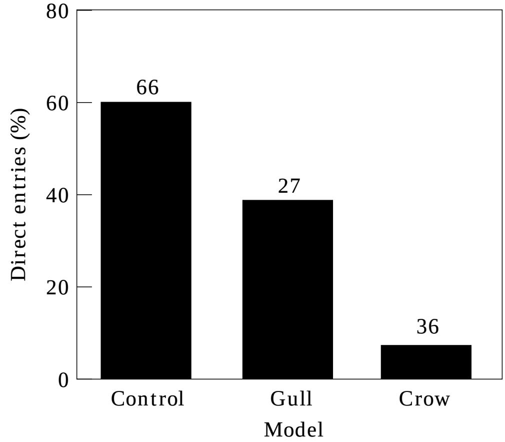

Figure 2. Percentage of nest entrances that were direct (as opposed to birds flying to a nearby perch and walking inconspicuously the rest of the way) in female Savannah sparrows when model predators were placed 5 m from the nest. Sparrows were less likely to enter their nests directly in the presence of crow models than in the presence of gull models (chi-square test; $P<0.05$). N trials given above bars.

Sparrows nesting during the first half of the breeding season took more time to enter their nests in the presence of a model predator than did sparrows nesting later in the season (6.8 ± 11.3 min, $N=94$ trials versus 3.9 ± 9.6 min, $N=52$, respectively; ANOVA; $P=0.04$). The seasonal decrease in 'wariness' was paralleled by a seasonal decrease in predation risk: daily survival rates and the proportion of nests fledging young were significantly higher during the second half of the breeding season as the vegetation became taller and denser (concealing sparrow nests better) and gulls and crows foraged less frequently in the study area. Although individual sparrows were exposed to model predators for no more than 30 min and never saw the same model twice, sparrows may have become habituated to the presence of abundant live gulls and crows by the end of the breeding season, which could explain their seasonal decrease in 'wariness' towards the model predators. We found a (non-significant) tendency for sparrows nesting in areas where gull densities were intermediate–high (and therefore where the sparrows were routinely exposed to gulls) to take less time to enter their nests when presented with either a gull or a crow model than sparrows nesting where gull densities were zero–low (ANOVA; $P=0.09$, $N=146$).

Gull Responses to Crows and Crow Models

When gulls were presented with a crow model near their nests, 87.8% reacted noticeably to the model ($N=32$ trials). The most common responses by gulls were to call loudly and to swoop or charge the model; 62.5% of the gulls made physical contact with the model, giving it a blow with their feet in aerial attack or striking it with their beaks or chests in a ground attack. Gulls that reacted to the model did so an average of 24.0 ± 35.4 s after the model was placed near their nest. Gulls with eggs made physical contact with the model 42% of the time, and gulls with nestlings made contact with the model 84% of the time (chi-square test; $P<0.05$).

In 1994, we chanced to determine the response of gulls to another predator of Savannah sparrows, the American kestrel, in a short-lived experiment unrelated to this study (D. Harrington, personal communication). A mounted kestrel placed 5 m from a sparrow nest lasted less than 1 min before a gull attacked it, knocking its head off and destroying the mount.

DISCUSSION

In this study, we aimed to distinguish between two general hypotheses. The first hypothesis is that some birds have no option but to nest near predators; the other proposes that birds benefit by nesting near predators in certain situations and therefore deliberately nest there. We compared the characteristics of Savannah sparrows that nested near and away from predators, evaluated their reproductive success and examined aspects of their behaviour in the presence and absence of predators. Not surprisingly, birds had the greatest reproductive success when they nested in an isolated field where predators were rare. In the main study area, sparrows confronted two types of predators, one of them (herring gulls) abundant but relatively ineffective, the other (American crows) less common but highly effective. Under those conditions, sparrows that nested near gulls reproduced as successfully or better than sparrows that avoided gulls. Despite being surrounded by a dense population of predatory gulls, sparrows nesting near gulls did not suffer greater predation rates during the incubation and post-fledging period than sparrows nesting away from gulls, nor was their own survival or the condition of their fledglings lower. In fact, during the nestling period nesting near gulls was associated with significantly lower predation rates, which resulted in greater overall reproductive success.

Our data suggest that lower rates of predation on sparrow nests near gulls was mainly due to the protection that gulls provided from crows. We propose that sparrows had higher reproductive success near gulls because the gulls, in defending their own nests from predatory crows, effectively shielded the sparrows from more dangerous predators. The gulls' alarm calls in response to the approach of potential predators such as crows (as well as greater black-backed gulls, ravens and humans) also alerted incubating sparrows, enabling them to flush early from their nests and making the nests more difficult to find. We cannot rule out the possibility that the greater nest density of sparrows in habitats with few gulls made such areas more profitable places for crows to search. Such an effect would have resulted in higher nest-loss rates in such areas independent of direct protection by gulls (Martin 1988, but see Andren 1991).

Experiments with models demonstrated that sparrows recognized gulls as potential predators but considered crows a far greater threat, a distinction that was consistent with our observations that crows were more systematic in their nest hunting (N. T. Wheelwright & J. Mitchell, unpublished data). Certain aspects of the sparrows' precautions in the presence of different model predators (the similarity in alarm-calling rates before entering the nest and in the length of incubation shifts after entering the nest, the close proximity of their approaches to the models) indicated that the sparrows did not perceive of the models as posing a risk to themselves. This is in accord with the fact that we have never seen gulls, crows or ravens prey on adult birds from the ground. None the less, the sparrows reacted as though the model presented a risk to their eggs or nestlings, and behaved differently in the presence of different model predators.

Patterns of nest predation implicated crows as more important predators than gulls (e.g. heavy losses in blueberry patches, which gulls avoided, and the failure of gulls to discover artificial nests). Another indication of the relative ineffectiveness of gulls as predators is that Savannah sparrows sometimes nested successfully within 1 m of gull nests. We know of no reported cases of songbirds nesting conspicuously and successfully so close to crow nests, and egg predation has been shown to be higher near crow nests than away from them (Slagsvold 1980; Nilsson et al. 1985). Our observations and experiments demonstrated that gulls aggressively chased crows and other sparrow predators from the vicinity of their nests. Sparrows nesting near gulls were able to compensate for the elevated risk of gull predation on their eggs or nestlings by building their nests in microhabitats that gulls rarely frequented, such as goldenrod and blueberry patches. In the presence of a predator, they were also more cautious about entering their nests and more likely to approach the nest indirectly, presumably to reduce the risk of revealing the location of their nests. This study demonstrated that nesting near gulls may reduce predation on a sparrow's eggs and nestlings, but for adult sparrows themselves, there may be benefits in using gulls as shields or early warning systems against hawks, owls or other predators.

Given the net benefits of nesting near gulls, one might predict that sparrows would prefer such nest sites, and that, as a result, the density of nesting sparrows would be higher near gulls. We found that sparrows tended to avoid nesting near gulls, however. We can eliminate some explanations for this apparent paradox. First, gull density near a Savannah sparrow's natal nest and its adult nest were not correlated; i.e. the tendency to nest near gulls was apparently not a heritable trait or one influenced by a bird's experience as a nestling. Second, sparrows nesting near gulls were not necessarily inexperienced or subordinate to birds nesting away from gulls. They were indistinguishable in a variety of traits related to social status (body size, age, date of nesting). Another indication that nesting among gulls was not simply a characteristic of younger or subordinate birds was the fact that, once a sparrow selected a territory or general breeding site, it showed strong breeding philopatry, moving a median distance of less than 30 m between years regardless of gull density; males and females were equally philopatric (N. T. Wheelwright & R. A. Mauck, unpublished data).

Constraints on the Evolution of Nest Associations

The existence of protective nest associations between birds and their predators has been documented in a few cases (Burger 1984, Ueta 1994). What remains to be established is whether the behaviour patterns leading to such associations represent true adaptations. Although selectively advantageous under certain circumstances, such associations probably only rarely evolve. In our study, a predisposition to nest near gulls presumably has not evolved in Savannah sparrows because the heritable basis for such a trait appears to be low and the strength of directional selection favouring it relatively weak. Avoiding gulls and other large predators is almost certainly strongly an adaptive behaviour throughout most of the range of Savannah sparrows.

Gene flow from populations where predator avoidance is always favoured could easily override weak selection for nesting among predators at a particular site such as Kent Island. At most times in the lives of most birds, predators are a serious hazard, although they might provide a protection umbrella near the nest site (Drycz et al. 1981). The decision to nest near a predator requires overcoming innate and adaptive fears. With life expectancies of less than 2 years (Wheelwright & Rising 1993), Savannah sparrows and other short-lived birds may have insufficient time to learn that the enemy of one's enemy is one's friend.

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