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Do Northern Harriers (*Circus cyaneus*) choose nest sites adaptively?

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Northern Harrier (*Circus cyaneus*) nest success was studied in relation to habitat choices and availability from 1980 to 1982 in New Brunswick. Measurements of moisture, vegetation, and visibility at nest sites indicated that harriers most often used wet sites surrounded by cattails, with high visibility. Moisture and vegetation had a significant effect on nest success ($p < 0.03$), while visibility played no significant role. Discriminant analysis indicated that of the three variables, moisture was consistently the best predictor of nest success over 3 years ($\geq 64\%$). Paradoxically, the order of settling by females was weakly correlated with the quality of nest sites in these years, yet choice was not limited by availability. We suggest, therefore, that nest site selection was a compromise between a wet nest site, close proximity to optimum foraging habitat, and, for females, access to a mate with a high food provisioning rate.

SIMMONS, R., et P. C. SMITH. 1985. Do Northern Harriers (*Circus cyaneus*) choose nest sites adaptively? *Can. J. Zool.* **63**: 494–498.

Le succès de la nidation du busard Saint-Martin (*Circus cyaneus*) a été étudié en relation avec le choix et la disponibilité des habitats de 1980 à 1982 au Nouveau-Brunswick. La mesure de l'humidité, de la végétation et de la visibilité aux sites de nidation a révélé que les busards utilisent surtout des sites humides entourés de quenouilles et permettant une bonne visibilité. L'humidité et la végétation ont un effet significatif sur le succès de la nidation ($p < 0,03$), alors que la visibilité ne semble pas jouer de rôle significatif. Une analyse discriminante a révélé que, des trois variables, c'est l'humidité qui constituait le facteur le plus prédictif du succès de la nidation durant les trois ans ($\geq 64\%$). Paradoxalement, l'installation des femelles à un site n'avait qu'une faible corrélation avec la qualité des sites au cours de ces 3 ans, et pourtant le choix du site n'était pas limité par la disponibilité. Nous croyons alors que la sélection d'un site de nidation est le résultat d'un compromis entre l'humidité du site, la proximité à une source de nourriture optimale et, pour les femelles, l'accès à un partenaire capable de récolter rapidement de la nourriture.

[Traduit par le journal]

Introduction

Theoretically, ground-nesting birds are vulnerable to a greater variety of predators and, hence, are under a stronger selection pressure to choose safe nest sites than are tree- or cliff-nesting species. The influence of such pressure is obvious when it is relaxed and tree- or cliff-nesting birds become ground nesters. This has been noted in Bald Eagles (*Haliaeetus leucocephalus*) in Alaska (Sherrod *et al.* 1977), Merlins (*Falco columbarius*) and Kestrels (*Falco tinnunculus*) in Orkney (Newton 1976), and Peregrines (*Falco peregrinus*) in inaccessible bogs in Finland (Linkola and Souminen 1969) and Estonia (Kumari 1974). However, obligate ground nesters, which constantly face such pressures, have evolved four methods to avoid terrestrial predators. These are: (i) to nest on islands inaccessible to terrestrial predators (Cullen 1957; Lack 1968), (ii) to nest in large groups to cooperatively mob predators (Kruuk 1964; Elliot 1983) or to dilute the probability of predation (Wilkinson and English-Loeb 1982), (iii) to nest in close association with larger, predatory species which offer protection through defence of their own nests (Hecht 1951; Cade 1960; Kretschmar 1965; Kretschmar and Leonovich 1967; Wiklund 1982), and (iv) to nest in well-concealed, evenly spaced sites (Hockey 1982; Redmond *et al.* 1982; Skeel 1983).

Ground-nesting, semicolonial Northern Harriers are unusual in that they are not confined to islands, very rarely mob predators cooperatively (Simmons 1983a), gain no apparent advantage from nesting in close association with Short-eared Owls *Asio flammeus* (R. Simmons and P. C. Smith, personal observation), and often do not build well-concealed nests (e.g., Schipper 1978). The objectives of this study, therefore, were

(i) to identify which parameters of the nest site were related to nest success, (ii) to determine if females chose their nest sites in the order expected, i.e., the best remaining sites first, and (iii) to determine whether their choices were affected by the availability of the best sites.

Despite the vast literature on raptor populations, only three papers (Ames and Mesereau 1964; Ogden and Hornocker 1977; Newton *et al.* 1978) have dealt with the success of raptors in relation to their site choices. This is the first such attempt at identifying the important determinants of success in the harriers (*Circus* spp.).

Study area

The study took place on a 60-km² portion of the reclaimed Tantramar Marsh (45°53' N, 64°20' W) of New Brunswick. This wet, flat marsh is a mosaic of basically four field types: open-water duck impoundments surrounded by cattails (*Typha* spp.); damp, grazed pastures supporting blue joint grass (*Calamagrostis canadensis*) and prairie cord grass (*Spartina pectinata*); dry, annually hayed timothy (*Phleum pratense*) fields; and wet and dry abandoned fields supporting *Spirea latifolia*, Vetch (*Vicia* spp.), umbelliferans, and some timothy. Since it was drained and dammed some 320 years ago (Smith 1967), the Tantramar Marsh is no longer annually flooded by the spring tides of the Bay of Fundy.

Methods

Sixty-four nests were located on the marsh between 1980 and 1982. Eleven of these nests are excluded from the analysis of success in relation to habitat type since they failed for reasons unrelated to predation (i.e., disease, abandonment, and human interference). When each nest was first visited, three site parameters were assessed. They are defined as follows: (i) Moisture: dry (if no water was present within 1 m of the nest), wet (if water appeared at the nest site owing to the observer's weight), and very wet (if running or standing water

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was already present within 1 m of the nest): (ii) Vegetation: the dominant vegetative cover within 1 m of the nest was assessed by eye and included cattails (*Typha latifolia*, *Typha angustifolia*, and some *Phragmites communis*), marsh grasses (blue joint and prairie cord grass), alders (*Alnus rugosa* shrubs up to 2 m high and some willow *Salix* spp.), and spirea (low *Spirea* bushes and other low shrubby plants such as *Kalmia angustifolia*). (iii) Visibility was assessed from three equally spaced points about the nest by pacing in metres the distance from the nest at which R.E.S. (at 1.85 m) could just no longer see the nest's contents; the greater the sum of the three distances, the greater the cone of visibility from the air. For statistical analyses, the mean value for 1980 (10 m) was arbitrarily set to divide "concealed" nests (≤ 10 m) from "open" nests (> 10 m). The range of scores varied from 3 to 45 m.

For seven nests which were found late in the season when visibility scores would have changed, we used an estimate of visibility (i.e., above or below 10 m) based on our knowledge of vegetation types and early season visibility at other nests. This estimate was required as we wished to determine the choices available to a female harrier when first settling. It was unnecessary to estimate moisture categories, since ground moisture did not vary perceptibly within years. For the purposes of sample size adequacy, the cattail and marsh grass vegetation categories were grouped as "forbs" and alders and spirea were grouped as "shrubs."

Since possible associations existed between all parameters measured and we wished to determine the single most important parameter affecting success (and the one(s) most likely to be used as habitat cues by settling females), SPSS discriminant analysis (Nie *et al.* 1975) was used to find the best predictors of success and failure of all nests over 3 years. Categories were ranked as follows for inclusion in the analysis: dry, 0; wet, 1; very wet, 2; spirea, 0; alders, 1; marsh grass, 2; cattails, 3. Visibility scores were entered directly.

Successful nests were those that fledged at least one young and those that failed were assumed to have fallen victim to predators as long as (i) no starved or diseased chicks were present, (ii) our research activities had not obviously affected failure, (iii) the female had not abandoned the nest with chicks still present (found among late-settling harem females), and (iv) the nest's contents had disappeared all at once. In the latter case, shell fragments or a disrupted nest lining were sometimes evident, while feather quills and remains of talons marked the death of older chicks. Regular nest visits showed up nests in which eggs disappeared one by one (avian predation) and nests in which chicks disappeared one by one (starvation or disease). Five nests which we visited shortly before or during laying were later deserted, so we curtailed visits at this time.

Harrier nest site choices were examined in two ways. (i) To determine if harriers were "forced" into some nesting situations, nest site choices were related to the availability of sites. (ii) To determine if each pair was choosing the best remaining site, the order in which females chose sites was related to the quality of each site. Quality was based on the probability of nest success, calculated by summing arc sine transformations of the percentage successes in each of the measured parameters: moisture, vegetation and visibility. An example of these calculations is shown in Table 1.

To determine the order of settling, clutches were backdated to initiation dates using methods outlined in Simmons (1983a). Availability of nesting habitat was determined from aerial photographs and "ground truthed." Only the availability of moisture types could be calculated, as some vegetation types were too small to be mapped accurately.

Nesting density, which may affect the success of nests through increased predation (Weatherhead and Robertson 1977), was not analysed as harriers on the Tanramar Marsh nested at least 260 m apart, averaging a maximum of 930 m and a minimum of 840 m apart during the 3 years of study (Simmons 1983a).

Results

Despite large fluctuations in the density of breeding birds from 1 nest/2 km² in 1980 to 1 nest/5 km² in 1982 (Simmons

TABLE 1. An example ("Front Lake" nest)^a of the calculations used to determine nest site quality scores for all nests in 1980-1982

Parameter	Category	% Success ^b	Arc sine transformation
Moisture	Very wet	91	72.5
	Wet	86	68.0
	Dry	55	47.9
Vegetation	Cattails	88	69.7
	Marsh grasses	87	68.9
	Alders	60	50.8
	Spirea	56	48.5
Visibility	≤ 10 m	68	55.6
	> 10 m	81	64.2
Nest site quality score of "Front Lake" nest: moisture (68.0) + vegetation (50.8) + visibility (64.2) = 183.0			

^aCategories: moisture = wet; vegetation = alders; visibility > 10 m.

^bFrom percentages in Fig. 1.

1983b), the proportion of nests in each habitat category varied little between years (Table 2). In 1982, however, the proportion of nests in dry, open sites increased relative to previous years. This was probably due to a prolonged dry spell early in 1982 which retarded vegetation growth and left the marsh much drier. Based solely on the percentage frequency of use, the "preferred" sites overall were wet (42% of all nests) cattails (41%) of high visibility (53%).

Of the total number of nests failing, 17% of 30, 27% of 22, and 17% of 12 failed as a result of predation in 1980, 1981, and 1982, respectively. There was no significant difference in the number of predator-destroyed nests between years ($\chi^2 = 1.00$, $p > 0.1$).

Nest success and habitat type

Very wet and wet sites were significantly more successful than were dry sites ($\chi^2 = 7.3$, $p < 0.005$). Figure 1 indicates that very wet sites were more successful (91%) than those nests in wet (86%) or dry (55%) areas; this trend was consistent in all years.

Vegetational differences appeared to be less significant determinants of success than were moisture categories. Grouping vegetation types, nests in forbs were significantly more successful than those in shrubs ($\chi^2 = 6.3$, $p < 0.03$). A hierarchy in success existed (Fig. 1), with cattail sites exhibiting greater success (88%) than marsh grass (87%), alder (60%), or spirea (56%) sites. Contrary to expectations (Balfour 1962; Duebbert and Lokemoen 1977; Hamerstrom and Kopeny 1981), the most concealed nests were the least successful (Fig. 1), although not significantly so. Indeed, all four nests with visibility scores > 20 m were successful. We saw only two instances of aerial predation in 3 years, both of which occurred at concealed nests (7 and 7 m), when the adult females were absent from the area. This implies that concealment *per se* has little deterrent value and is strengthened by the observation that vigilant adults always chased away potential aerial predators near (≤ 150 m) their nest and did not need to select concealed sites to deter such predators (cf. Daeman and Lorij 1973).

Assuming that selection pressures in the form of terrestrial predators are intense enough to promote antipredator strategies, harriers should choose very wet cattail sites with high visibility. This prediction was verified (Table 2), although very wet sites were used slightly less than expected.

TABLE 2. The number and proportion (percent) of nests in each habitat category in 1980, 1981, and 1982

	Moisture			Vegetation				Visibility	
	Very wet	Wet	Dry	Cattails	Marsh grasses	Alders	Spirea	≤10 m	>10 m
1980	8(27)	13(43)	9(30)	10(33)	9(30)	6(20)	5(17)	16(53)	14(47)
1981	4(18)	10(45)	8(36)	10(45)	2(9)	0	10(45)	11(50)	11(50)
1982	2(17)	4(33)	6(50)	6(50)	3(25)	0	3(25)	3(25)	9(75)
Total	14(22)	27(42)	23(36)	26(41)	14(22)	6(9)	18(28)	30(47)	34(53)

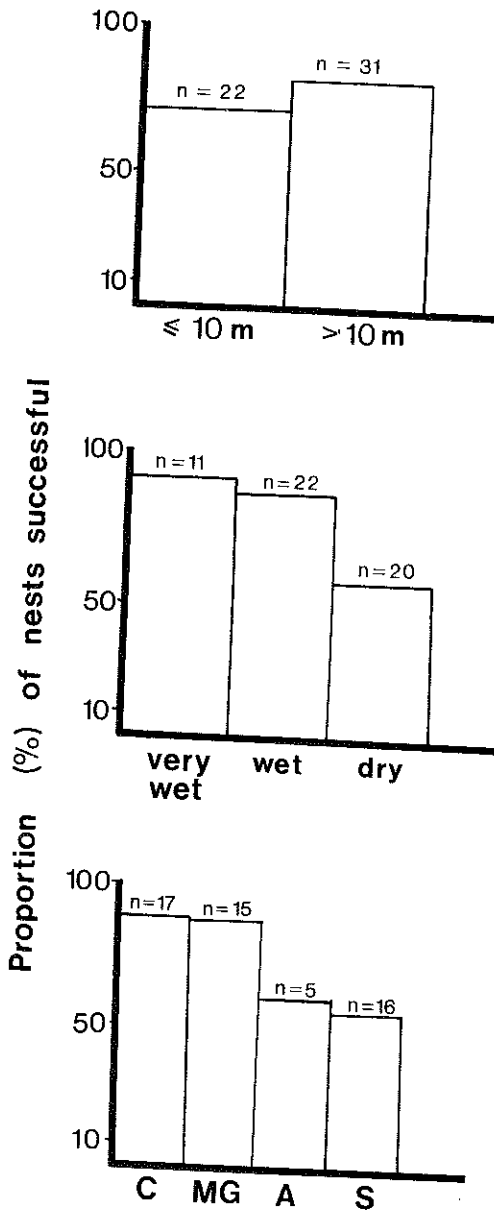


FIG. 1. Harrier nest success (fledged ≥ 1 young) in relation to visibility (top), moisture (middle), and vegetation (bottom) at the nest site. Vegetation: C, cattails; MG, marsh grass; A, alder; S, spirea.

Importance of moisture, vegetation, and visibility in nest success

Since significant differences in success were obtained in both moisture and vegetation categories and we wished to define the most important parameter in terms of female choice,

TABLE 3. The best discriminators of nest success as determined by SPSS discriminant analysis

Year	Parameters entered	Parameters used	Roa's V (p)	No. (%) of nests correctly classified
1980	Moisture	Moisture	3.35(0.07)	21(81)
	Vegetation	Vegetation	7.64(0.006)	
	Visibility	Visibility	2.04(0.2)	
1981	Moisture	Moisture	7.65(0.006)	14(82)
	Vegetation			
	Visibility			
1982	Moisture	Moisture	1.60(0.2)	7(64)
	Vegetation			
	Visibility			
All years	Moisture	Moisture	11.66(0.0006)	40(74)
	Vegetation	Vegetation	3.17(0.07)	
	Visibility			
All years	Moisture	Moisture	11.66(0.0006)	39(72)

discriminant analysis was used to separate the effect that each had on success. As expected, moisture and vegetation were the most important predictors of success (Table 3). However, moisture alone consistently correctly classified the greatest number of nests within years and between years. The percent correctly classified varied from a minimum of 64% in 1982 (the driest year) to 82% in 1981. Combining all three years, moisture classified a highly significant (Rao's V = 11.6, $p < 0.0006$) number of nests correctly (72%). Essentially, this means that a harrier could greatly minimize the chances of nest failure by choosing a nest site on the basis of moisture alone.

Nest site quality and order of choice

Although moisture was the best predictor of success, all three parameters appeared to play minor roles in different years (Table 3). A unique quality score was therefore calculated for each nest, based on the combination of features measured at the nest.

If, as predicted by natural selection, harriers choose the highest quality nest sites first, a strong negative correlation should exist between the settling order and quality scores. Paradoxically, this was not found. Spearman rank tests indicated that in all 3 years, the trend was in the required direction but only weakly correlated ($r_{1980} = -0.25, p < 0.3; r_{1981} = -0.2, p < 0.1; r_{1982} = -0.2, p < 0.1$). Using only moisture, the results were almost identical ($r_{1980} = -0.12, p < 0.1; r_{1981} = -0.2, p < 0.1; r_{1982} = -0.2, p < 0.1$). Based on this analysis, harriers did not appear to be choosing nest sites primarily to minimize predation, even though the consistently

negative correlations suggest that their choices were loosely associated with high moisture levels. Such a result could arise because of a more important selection pressure acting on harriers or because their choices were limited by the availability of sites.

Nest site choice and availability.

To ensure that some females were not limited by a paucity of the best sites, we calculated the maximum number of sites theoretically available, assuming that each female required a territory at least 375 m in diameter (Simmons 1983a). The number of possible wet:dry territories was 127:145 (within suitable vegetation types). Wet to dry nest sites were used in a ratio of 41:23 (Table 2). Therefore, not only were wet sites not limited, but they were used significantly more than expected based on chance alone ($\chi^2 = 6.6$, $p < 0.02$). This analysis shows that harriers clearly preferred wet nest areas relative to their availability and that the order of settling was not apparently affected by availability.

Discussion

Northern Harriers lay white eggs, build relatively exposed nests, do not cooperatively mob predators, and yet suffer relatively low rates of predation. The behaviour of the adults in chasing off aerial predators and their choice of nest sites clearly show that egg colour, nest exposure, and cooperative mobbing of predators are probably of little importance in deterring predators. The two factors which were important in deterring predators were the constant vigilance of the adults and, perhaps most important, the choice of a wet nest site to minimize terrestrial predation. Not only did the choice of a very wet site raise the probability of success to over 90% for harriers on the Tantramar Marsh, but harriers clearly preferred wet areas relative to their availability. Why, then, did females not settle in the order predicted by natural selection? A possible reason is that they could not correctly or accurately assess future levels of moisture early in the season. This is unlikely, however, as moisture did not vary either during the period that females were settling or later in the season. Were other stronger selective pressures at work? Two possibilities that have been explored elsewhere (Simmons 1983a) were (i) female proximity to a prime foraging area and (ii) access to a mate with a high food provisioning rate, regardless of nest site placement. Partial support for (i) comes from the fact that 10 of 30 nests constructed in 1980 were located within 250 m of areas of high vole (*Microtus pennsylvanicus*) abundance and low cover, yet in 1981, when voles had moved out of these areas, these nest sites were either relocated further afield ($n = 2$) or had disappeared altogether ($n = 8$). All 1981 nests were adjacent to the best remaining food sources. Support for (ii) comes from the strong correlations found between the settling order of females and the rate at which their mates provided food for them. This was true in both years in which it was studied (Simmons 1983a, in preparation). Based on these two results, we believe that nests were probably positioned as a compromise between close proximity to food sources and a low risk of predation.

Nesting habitat preferences of harriers, based on the frequency of use, have been reported by Balfour (1962), Schipper (1978), and Hamerstrom and Kopeny (1981), although nest success was not examined. In Orkney (Balfour 1962), only 10 of 290 nests were constructed in dry areas, while the most frequently used vegetation consisted either of heather (*Caluna vulgaris*) in association with rushes (*Juncus* spp.) (189 nests),

rushes alone (52 nests), or heather alone (40 nests). Hamerstrom and Kopeny (1981), analysing nest site selection in a drained marsh in Wisconsin, found that 45% of 176 nests had grasses (Graminae) or willow as the dominant vegetation within 60 cm of nests. When the willow habitat decreased in area, harriers moved to an increasingly abundant *Spirea* habitat. *Circus cyaneus* in the Netherlands preferred "humid or dry ground" on which to nest, the wettest niche being utilized by the sympatric marsh harrier (*Circus aeruginosus*) (Schipper 1978). Where these harriers are not sympatric (Orkney and North America), *C. cyaneus* appears to prefer the wet sites, while sympatry is associated with *C. cyaneus* using drier sites (Schipper 1978). This may arise from competitive exclusion.

The significantly greater success of nests in wet sites in this study is probably a result of the differential habitat preferences of suspected mammalian predators that occurred on the marsh (red fox, *Vulpes vulpes*; striped skunk, *Mephites mephites*; racoon, *Procyon lotor*; feral cat, *Felix domesticus*; American mink, *Mustela vison*; and stoat, *Mustel erminea*). Only the racoon and the American mink were seen in marshy areas (R. Simmons and P. C. Smith, personal observation); thus, harrier nests may be at risk from fewer predators in wet areas. That the most visible sites tended to be more successful (Fig. 1) suggests that mammalian predators either foraged in dense vegetation or that they were vulnerable to the fast, shallow attacks of adult harriers in open situations. Marsh-breeding Red-winged Blackbirds (*Agelaius phoeniceus*) in the most visible sites were also shown to exhibit higher breeding success than other birds (Weatherhead and Robertson 1977), but no explanation was given.

If the results reported here are true reflections of the preferences of harriers for wet nest sites, logically, wet marshes should be more productive than dry ones. A comparison is possible between the predominantly wet Tantramar Marsh and the dry Buena Vista Marsh of Wisconsin (Hamerstrom 1979). The Buena Vista Marsh supports willows, *Spirea*, grasses, and *Carex* spp., and is defined as a "nonmarshy grassland" (Hamerstrom and Kopeny 1981). The Tantramar Marsh supports similar vegetation types plus marsh grasses and cattails (see Methods). It is approximately 53% drained by area. The 163-km² Buena Vista Marsh supports an annual mean density of 0.77 harrier nests/10 km² (Burke 1979), while the 60-km² Tantramar Marsh supports a yearly mean density of 3.50 nests/10 km² (Simmons 1983b). The "wet" Tantramar Marsh thus has a nesting density nearly five times that of the Buena Vista Marsh. Since productivity per female was identical on both marshes (Burke 1979; Simmons 1983a), the total productivity of the wetter marsh was five times that of the drier one. A possible factor limiting nesting density on the Buena Vista Marsh may therefore be the paucity of habitat "islands" suitable for harrier nests. However, food cannot be divorced from a discussion of habitat selection and it is equally plausible that because the harriers' principal prey (*Microtus pennsylvanicus*) also prefers damp areas in which to forage and breed (Getz 1970; Birney et al. 1976; R. Simmons, in preparation), a damp marsh may be more productive for harriers because of both its vole population and the number of habitat islands suitable for nesting.

In conclusion, the harriers of the Tantramar Marsh showed significantly greater nesting success when their nests were situated in the wettest sites, while vegetation type and visibility made little difference to success. Although natural selection predicts that the highest quality sites should be chosen first, this

was not the case in this study. Other selection pressures involving food were suggested as the probable cause of this anomaly, since availability of nest sites and an alteration of moisture levels following the settling of breeding females could not be implicated.

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