Nesting success, density, philopatry, and nest-site selection of the Whimbrel (*Numenius phaeopus*) in different habitats

MARGARET A. SKEEL[1]
Department of Zoology, University of Toronto, Toronto, Ont., Canada M5S 1A1
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A population of Whimbrels (*Numenius phaeopus*) that nested in three distinct habitats near Churchill, Manitoba, was studied from 1973 to 1976. Nest success in the hummock–bog habitat was 86% and was significantly higher than the 54% success in each of the sedge–meadow and heath–tundra habitats. The hummock–bog habitat differed from the other two in several other respects. In the hummock–bog habitat, density of nesting pairs was highest and averaged 0.11 pairs/ha. Distribution of nests tended toward uniform. Density in sedge–meadow and heath–tundra habitats averaged 0.04 and 0.05 pairs/ha, respectively. Philopatry of banded adults to the hummock–bog habitat was considerably higher than to the other two, indicating more stability there. Several attributes of nest placement were important, and the hummock–bog habitat, structurally the most complex, offered more potentially favorable sites. The higher nesting success in the hummock–bog habitat was attributed primarily to the more complex structure of this habitat (crypticity is enhanced) and the higher nesting density (predation is reduced through joint defense).

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Une population de courlis hudsoniens (*Numenius phaeopus*) qui a établi des aires de nidation en trois habitats différents de Churchill, Manitoba, a fait l'objet d'une étude de 1973 à 1976. Le succès de la nidation dans l'habitat "tourbière en dôme" a été évalué à 86%, valeur significativement plus élevée que le succès de nidation de 54% enregistré dans les habitats "prairie à laîches" et "toundra à éricacées." L'habitat "tourbière en dôme" diffère des deux autres par d'autres aspects également: la densité des couples qui construisent des nids y est plus grande (0,11 couples/ha en moyenne). La répartition des nids tend vers l'uniformité. La densité des couples dans les autres habitats est de 0,04 dans la prairie et de 0,05 couples/ha dans la toundra. La fidélité des adultes rayés à l'habitat "tourbière en dôme" est beaucoup plus forte que la fidélité aux deux autres habitats; il y a donc plus de stabilité dans ce milieu. Plusieurs facteurs sont importants lors du choix d'un site de nidation et l'habitat "tourbière en dôme," dont la structure présente le plus de complexité, offre plus de sites adéquats. Le succès plus grand de la nidation dans cet habitat est attribuable d'abord à sa structure plus complexe (le camouflage y est plus facile) et à la densité plus grande des nids (la prédation est moins grande grâce aux efforts conjoints de défense).

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Introduction

Many species of birds utilize different habitats for nesting. Studies of breeding success and density in different habitats have suggested that habitats vary in quality and that high-quality habitats, by definition, have high productivity (e.g., Kluyver and Tinbergen 1953; Glas 1960; Nettleship 1972; Robertson 1972; Zimmerman 1982). Differences often included greater nest-site availability, better food resources, and enhanced predator and climatic protection from the vegetation or physical structure. Breeding dispersal (movement between successive breeding sites) can also be associated with quality of nesting areas and reproductive success (Greenwood 1980).

Differences in nest-site selection are often concomitant with choice of habitat. A nest site is chosen with preference for locations where protection from predation and climatic conditions are maximized (e.g., MacLean and Moran 1965; Hadley 1969; Verheyen 1969; Bongiorno 1970; Schaefer 1976). Quality of sites with respect to these preferences will vary with habitat.

In my study area, Whimbrels (*Numenius phaeopus*) nested in three distinct habitats. I endeavored to determine if nesting success was dependent upon habitat and, if so, what effect this had on density, distribution, and breeding dispersal. Important parameters of nest-site selection were also measured and these were related to habitat.

Study area

The study area, near Churchill, Manitoba, lies within the Hudson Bay Lowlands, a region of low relief, poor drainage, permafrost, and numerous shallow lakes and ponds. The climate is strongly affected by Hudson Bay. In 1973 and 1974 the average daily mean temperatures for May, June, and the

[1]Present address: 4147–122 Street, Edmonton, Alta., Canada T6J 1Z1.

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first half of July were 3, 5, and 8°C, respectively. Plant species of the area are listed by Ritchie (1956) and Scoggan (1959).

The Whimbrel's North American breeding range lies within the Low Arctic and Subarctic zones. The Subarctic, including the Churchill area, is a transition zone where low-arctic tundra intergrades with stunted spruce–tamarack Boreal Forest. This intergrading has resulted in a diversity of habitats. I located Whimbrel nests in three distinct habitats: (1) hummock–bog, (2) sedge–meadow, and (3) heath–tundra.

Hummock–bog habitats are low areas characterized by sparsely scattered or clumps of stunted spruce (*Picea mariana*) and tamarack (*Larix laricina*) and by patches of small hummocks (<30 cm high) intermingled with patches of large lichen-covered hummocks up to 75 cm high. Dwarfed shrubs such as *Betula glandulosa* and *Rhododendron lapponicum* are abundant. In late May and early June much of the area is under several centimetres of standing water except for the isolated and adjoining hummocks. This habitat is the most structurally complex and patchy of the three habitats owing to the large hummocks, less continuous vegetation cover, and higher density of scattered shrubs and trees.

Sedge–meadow habitats are low, wet areas without relief or trees and have a continuous ground cover of grasses and sedges (e.g. *Carex* spp.) with scattered emergent shrubs.

Heath–tundra habitats are gently rolling high, dry, treeless areas characterized by a dense ground cover of lichens (*Cladonia* spp.) and associated low vegetation and scattered ground-hugging dwarfed shrubs (e.g. *Saxifraga oppositifolia*).

Methods

The study spanned the breeding seasons of 1973 and 1974 (mid-May to late July) and a major portion of the 1975 and 1976 nesting period (mid-June to early July). Each year 30–35 nests were located, and in 1973 and 1974 nests were followed to their final outcome. I located nests throughout the incubation period in all habitats. Visits to nests averaged about once every 10 days until late June. On more frequent visits to territories, scolding by a bird indicated that the nest was intact. In late June and early July when hatching occurred, nests were visited every 1–4 days. Eggs considered to have successfully hatched were last observed either as chicks, in a stage of pipping in a nest with chicks, or showed evidence of having hatched between visits during the hatching period (three nests).

The nesting period was considered to end immediately after hatching of eggs. Nesting success was determined using the Mayfield (1961, 1975) nest-exposure method. The mortality rate r was calculated by dividing nests lost by nest days. The daily survival rate was then $1 - r$. The formula for standard error of the daily survival rate was developed by Johnson (1979).

The patchy distribution of habitats resulted in several study plots: four in heath–tundra habitats of 14–74 ha; four (three in 1973) in sedge–meadow habitats of 23–142 ha; and one in the hummock–bog habitat of 166 ha. Several hummock–bog nests located outside the plot were excluded from density estimates but were included in nesting success and philopatry. Locating all nesting pairs within a plot in 1973 and 1974 was possible because Whimbrels flew from the nest or near it towards me when I was 50–250 m away and scolded until I left. The approximate location of three nests was based on adult behavior. All plots were visited at least once in the first half of the nesting season.

In 1973 the hummock–bog plot was photographed from a height of 610 m after clutches had hatched and each nest was marked with a 4-m arrow. An accurate map of the nests was traced from the prints (scale 1:8000). The 1974 nests were mapped by measuring the direction and distance of each nest with a tape measure from one or two of the 1973 nests. Distances to nearest neighbors were measured from the maps. The area of the plot was estimated by superimposing the map on a 1-mm grid. Distances to nearest neighbors in sedge–meadow and heath–tundra plots were measured with a tape measure, and areas were determined using a 1 : 50 000 map and 1-mm grid.

Adults were marked with a regulation aluminum band and colored bands. Loss of colored bands was high so all recoveries were trapped to read the aluminum band. Adults were nest-trapped late in the incubation period by using a wire funnel-door trap 50 cm across and 25 cm high. The bird was usually on the eggs within 15 min of my withdrawal. A 25-cm-high wire fence was placed around 39 nests with eggs in a late stage of pipping (four nests were deserted). The chicks were enclosed in an area 2 m across for a day or less and were banded with a regulation band.

Each year the study plots were searched with similar effort relative to density for nests and banded birds. Locations of nest sites were noted or marked. Distances between successive sites of a returning Whimbrel were measured with a tape measure or, if ≥1 km, on a 1:50 000 map. Determination of sex followed Skeel (1982).

In 1973 and 1974, after clutches hatched, seven parameters were measured at each nest and a corresponding random site. The latter was determined using a table of random numbers to select one of eight directions and the distance in paces (up to 99) from the nest. Percent vegetation cover within 1 m was estimated using a 1-m grid divided into 10-cm squares and laid four times with a corner on the site. Sokal and Rohlf (1969) was consulted for statistical tests.

Results

Nesting success

A nest success is defined as the survival of at least one egg from the nest and is distinguished from egg success, the probability that an egg will produce a chick. Nest success did not differ significantly between 1973 and 1974 in hummock–bog and sedge–meadow habitats ($\chi^2_{1\ df} \le 0.04$, $P > 0.5$), and therefore data for the 2 years were pooled. The estimated daily survival rate of a nest in the hummock–bog habitat was significantly higher than in sedge–meadow habitats ($P < 0.05$) and, to a lesser degree, than in heath–tundra habitats ($P < 0.1$, Table 1). The low significance level in the latter comparison is likely due to the small sample size for heath–tundra habitat.

The survival rate of a nest for 24 days, the

TABLE 1. Nest and egg success of the Whimbrel in three habitats near Churchill, Manitoba

	Habitat		
	Hummock–bog	Sedge–meadow	Heath–tundra
No. of nests	38	19	8
No. of nest days without losses	481.5	234.5	117.5
No. of nests lost (nest days with losses)	3	6	3
$\chi^2_{df=1}$	← 4.61** → (Hummock–bog vs. Sedge–meadow)		
	← 3.44* → (Hummock–bog vs. Heath–tundra)		
		← 0.00^{ns} → (Sedge–meadow vs. Heath–tundra)	
Estimated daily survival rate of a nest ($\hat{s}$)	0.994	0.974	0.974
SE of $\hat{s}$	0.0036	0.0103	0.0146
(A) Hatching rate in persisting nests (n = 167 eggs)	0.958	0.958	0.958
(B) Probability of an egg surviving 24 days in a persisting nest	0.934	1.000	1.000
(C) Nest success (nest survival rate for 24 days)	0.861	0.537	0.538
Egg success ($A \times B \times C$)	0.770	0.514	0.515

NOTE: *ns*, not significant ($P > 0.9$); *, $P < 0.1$; **, $P < 0.05$.

TABLE 2. Nesting densities of the Whimbrel and distance to nearest neighbor in three habitats near Churchill, Manitoba

Habitat and year	No. of pairs	No. of study plots[a]	Total area (ha)	No. of pairs/ha	Mean distance to nearest neighbor (m)[b]	Expected mean distance if dispersion is random (m)	R[c]
Hummock–bog habitat							
1973	19	1	166	0.115	201.4 (18.6)[d]	148.0 (17.7)	1.36**
1974	17	1	166	0.102	226.8 (22.1)	156.4 (19.8)	1.45**
Overall	36		332	0.108	213.4 (15.1)		
Sedge–meadow habitat							
1973	9	3	184	0.049	374.0 (40.4)		
1974	10	4	342	0.029	242.5 (28.9)		
Overall	19		526	0.036	293.1 (29.5)		
Heath–tundra habitat							
1973	7	4	145	0.048	286.0 (44.3)		
1974	1	4	145	0.007	—		
Overall	8		290	0.028	286.0 (44.3)		

NOTE: **, there is a highly significant ($P < 0.01$) deviation of the dispersion pattern from random towards maximum spacing.
[a]In 1973, all study plots had at least one nesting pair. In 1974, no pairs nested in one sedge–meadow and three heath–tundra plots that had been used in 1973.
[b]Nests near the periphery of the plots were excluded if there was the possibility of a nest outside the area searched being the nearest neighbor. The number excluded were sedge–meadow 1973, 4; 1974, 2; heath–tundra 1973, 2.
[c]R is the measure of departure from a random distribution and can vary from 0 (maximum aggregation) to 2.1491 (maximum spacing). In a random distribution R = 1.
[d]Numbers in parentheses are SE.

approximate incubation period (Skeel 1976*a*), was 86% in the hummock–bog habitat compared with only 54% in each of the other habitats. Nest loss was due to predation, primarily by avian predators. The Herring Gull (*Larus argentatus*) appeared to be the major predator, with others including the Common Raven (*Corvus corax*), Thayer's Gull (*L. thayeri*), Parasitic Jaeger (*Stercorarius parasiticus*), and possibly Shorttail Weasel (*Mustela erminea*) and Red Fox (*Vulpes fulva*).

Egg success was slightly lower than nest success because some eggs did not hatch and a few were lost from persisting nests. Six of 167 (3.4%) eggs observed at hatching were infertile (three in the hummock–bog habitat). One egg with a well-developed embryo was found squashed in a nest. In the hummock–bog habitat, a single egg was lost at five persisting nests and all eggs were lost at three nests. In the other habitats, there was total egg loss at all nine nests where predation occurred.

Observer interference was excluded from the above results. Two of 65 nests were deserted after about my

TABLE 3. The number of adult Whimbrels banded, examined for bands, and recovered from 1973 to 1976

Year	No. of pairs located × 2	No. of birds examined for bands	No. of examined birds with a band from a previous year (A)	No. of new birds banded (B)	No. of known banded birds ($A+B$)	No. of known banded birds recovered in: 1974	1975	1976
			Hummock–bog habitat					
1973	38	38	0	15	15a	3	8c	6
1974	22	16	3	5	8b		3d	4
1975	38	37	11	11	22			11
1976	32	28	11	14	25			
			Sedge–meadow and heath–tundra habitats					
1973	32	32	0	16	16a	0	1c	3
1974	22	12	0	3	3b		0d	1
1975	28	27	1	1	2			1
1976	26	24	5	15	20			

NOTE: a, b, c, d refer to Bailey's small-sample formula for calculating return rate ($bc/a(d+1)$); see text).

second visit to the nest vicinity. Possibly other deserted nests were missed. Three of 35 nests were deserted after nest-trapping one adult, and one egg was broken by a trapped adult.

Nesting densities and dispersion

The overall density of pairs in the hummock–bog habitat was three to four times higher than in the other habitats (Table 2). Also, the distance between a nest and its nearest neighbor averaged closer in the hummock–bog habitat at 213.4 m (range = 70–476 m) than in the other two (range = 130–480 m). An analysis of variance revealed a significant difference among the habitats in the overall mean distances to the nearest neighbor ($F_{2,51\ \mathrm{df}} = 3.96$, $P < 0.05$). There was no significant difference between mean distance in sedge–meadow and heath–tundra habitats ($t_{16\ \mathrm{df}} = 0.13$, $P > 0.09$), and thus, the difference lies in the closer mean distance in the hummock–bog habitat. Once in each of the sedge–meadow and heath–tundra habitats, a pair was the sole nester within the entire expanse (with areas of 46 and 16 ha, respectively).

The hummock–bog plot was a discrete area of 166 ha enclosed by tree line and two roads. The dispersion pattern of the nests there was determined following Clark and Evans (1954, Table 2). For 1973 and 1974 the mean distance between a nest and its nearest neighbor was significantly greater than expected if the distribution of nests were random ($P < 0.01$). Thus spacing of nests tended toward a uniform pattern. Nests were too few in any sedge–meadow or heath–tundra plot to determine dispersion pattern.

Philopatry

Recovery of adults in hummock–bog habitat was relatively high, but in sedge–meadow and heath–tundra habitats it was low (Table 3). Of the 31 adults (13♂, 14♀, and 4?) banded in the hummock–bog habitat from 1973 to 1975, 14 (8♂, 4♀, and 2?) were recovered there at least once between 1974 and 1976. Of 20 (4♂, 10♀, and 6?) banded in the other two habitats, six (2♂, 3♀, and 1?) were recovered there and two (♀) in the hummock–bog habitat. The fate of the 29 birds not recovered is unknown.

Return rates from one year to the next were estimated using Bailey's small-sample formula (Ricker 1975, p. 129). In this triple-catch method, birds are marked during two breeding seasons, and return rates are calculated from recovery data obtained during the third season. By using the formula return rate = $bc/a(d+1)$ (letters correspond to Table 3) for the 1973–1974 interval and parallel comparisons for the next yearly interval, estimated return rates averaged 99% (approximate variance = 30%) for the hummock–bog habitat but only 26% (approximate variance = 7%) for the other two habitats combined. These are only approximations because small samples of birds were involved and variances are high. However, the data strongly indicate higher philopatry by birds to hummock–bog habitat.

Of the 22 recovered adults, 20 renested within 400 m of their previous nest site, thereby occupying all or part of their former territory. The mean distance between successive nest sites did not differ significantly among habitats ($F_{2,17\ \mathrm{df}} = 2.89$, $P > 0.05$) and overall averaged 156.4 m ($n = 20$, SE = 15.66, range =

TABLE 4. A comparison of nest sites of the Whimbrel and random sites in three habitats

Habitat	Type of site (n)	Distance to nearest shrub (cm)		% vegetation cover within 1 m		% on a hummock	
		Mean (SE)	t or U^a	Mean (SE)	t or U	%	G_{adj}
Hummock–bog	Nest (40)	49.8 (11.15)	$t = 1.84^{ns}$	64.8 (3.47)	$t = 2.39$*	92.5	38.65**
	Random (40)	62.2 (13.92)		48.6 (4.81)		25.0	
Sedge–meadow	Nest (19)	32.0 (8.38)	$U = 304.5$**	71.3 (4.80)	$U = 248.0$*	94.7	20.43**
	Random (19)	138.2 (28.06)		55.8 (4.89)		21.1	
Heath–tundra	Nest (8)	235.0 (153.57)	$U = 38.0^{ns}$	93.6 (2.61)	$U = 33.5^{ns}$	12.5	-0.004^{ns}
	Random (8)	209.3 (94.36)		87.9 (3.60)		0.0	

NOTE: Differences between means were tested using Wilcoxon's two-sample test: in cases where $n > 20$, a t-statistic was calculated. Differences between percentages were tested using the G-statistic and Yates' correction. Significance: **, highly significant ($P < 0.005$); *, significant ($P < 0.05$); ns, not significant.

41–376 m). In the hummock–bog habitat, three adults (♂) captured all 4 years nested close to all previous sites, as did three adults (1♂, 2♀) captured 3 of the 4 years. (For each of these birds, the distance between successive nest sites was calculated as the average of all possible combinations between two sites.) One adult (♂) changed habitat but likely maintained much the same territory, moving 67 m from a sedge–meadow to an adjacent heath–tundra habitat. It is noteworthy that 2 (♀) of the 22 recovered adults moved distances of about 5250 and 6600 m from a sedge–meadow to the hummock–bog habitat. They were recovered after 1 year (had nested unsuccessfully) and 2 years (had nested successfully), respectively.

Mate fidelity occurred in three of five pairs banded in the hummock–bog habitat. These three retained their mates from 1975 to 1976. The males of two pairs had new unbanded mates when recovered after 1 and 2 years. Of a pair banded in a sedge–meadow habitat in 1973, the female was recovered in the hummock–bog habitat in 1975 with an unbanded mate. The fate of the initial mates for the latter three pairs is unknown.

Few Whimbrels banded as chicks were recovered. Of 71, 50, and 14 chicks banded from 1973 to 1975, respectively (45, 37, and 14 in the hummock–bog habitat), only two (♂) were recovered as adults. Both were banded in the hummock–bog habitat in 1973 (at different nest sites) and were recovered there in 1976 nesting about 1000 and 1630 m from where they hatched.

Nest-site selection

The presence of a shrub within 1 m of the nest was characteristic (Table 4). Shrubs were most abundant in the hummock–bog habitat. The mean distance from random sites to the nearest shrub was significantly less there (Kruskal–Wallis $H = 8.0$, $P < 0.05$), and random sites did not differ significantly from nest sites ($P > 0.05$). However, in sedge–meadow habitats where shrubs were more widely distributed, nests averaged significantly closer than random sites to the nearest shrub ($P < 0.005$). In heath–tundra habitats, where shrubs were not readily distinguishable from the ground vegetation, nest and random sites did not differ significantly ($P > 0.05$).

In hummock–bog and sedge–meadow habitats, the vegetation cover at nests was significantly greater than the cover of about 50% at random sites ($P < 0.05$, Table 4). In heath–tundra habitats, ground cover was uniformly high.

A prominent feature of nests was the use of hummocks or, to a lesser degree, hummock ridges (both referred to as hummocks here). Nest sites occurred significantly more often on hummocks than did random sites in hummock–bog and sedge–meadow habitats ($P < 0.005$). There was no difference in the almost hummock-free heath–tundra habitat. Of the 67 nests, 56 (84%) were on hummocks, these usually being 30–75 cm high in the hummock–bog habitat and 10–20 cm in the other habitats. Six nests were on flat heath–tundra, four among sedges, and one on gravel.

Nest sites located on the side of or low in a larger hummock or adjacent to a shrub were afforded protection from the wind. A site was considered protected from one or more of eight compass directions if the adjacent mound of hummock or shrub was ≥8 cm above the nest cup. From 16 May to 15 July of 1973 and 1974, the maximum daily wind velocity occurred from N, NE, or E 69% ($n = 124$ days) of the time. Wind protection at nest sites ($n = 147$ directions), but not at random sites ($n = 57$ directions), was also predominantly from these directions. Protected directions at nests correlated significantly with daily maximum wind direction (Kendall coefficient of rank correlation = 48, $P < 0.01$). Protected directions at random sites did not correlate with wind direction or protected directions at nest sites (Kendall coefficient = 6, $P > 0.05$). Protection from at least one of N, NE, or E occurred at 73% of the 67 nests. Nine nest and 32 random sites were not protected, and some sites had protection from more than one direction.

Nest and random sites did not differ significantly ($P < 0.05$) within any habitat for distance to the nearest water at the time of nesting, distance to the nearest tree ≥2 m high, or the number of trees ≥2 m high within 30 m.

Discussion

Nesting success: its relationship to habitat structure and density

Because productivity is the ultimate measure of habitat quality, the hummock–bog habitat, where nesting success was highest, was the optimal of the three. The nesting success there of about 86% fell within the range of 66–96% found for five other scolopacid species (Ricklefs 1969). Predation of eggs, almost the sole source of egg loss, was lowest in the hummock–bog habitat probably because of two advantages of nesting there: (*1*) enhanced crypticity of the nest and incubating bird owing to more complex and irregular habitat structure; and (2) more effective protection from predators through joint effort in detecting and chasing a predator. These two factors comprise the main antipredator nest defenses of the Whimbrel against primarily avian predators.

The nest and incubating bird are probably least conspicuous in the hummock–bog habitat owing to the disruptive effect there of abundant prominant hummocks, patches of unvegetated ground, scattered trees, and a high density of shrubs. Because Whimbrel eggs are large and exposed to view from above, nests are likely more conspicuous to avian predators in the relatively monotonous sedge–meadow and heath–tundra habitats. Conspicuousness of nests in habitats of varying structure has not been tested. White-fronted Plover (*Charadrius marginatus*) nests placed among conspicuous objects may be rendered less conspicuous because of the disruptive effect of nearby objects (MacLean and Moran 1965).

Possibly because of enhanced crypticity and more favorable nest sites, the hummock–bog habitat has attracted more nesting pairs. The higher density increases joint effort in detecting and chasing a potential predator (the *short* and *long predator alarm calls*; Skeel 1978). Whimbrels are aggressive and were often observed to chase potential predators from their territories. Once initiated, a chase continued up to 500 m and was often joined by other Whimbrels nesting nearby.

Whimbrel eggs and incubating adults are camouflaged to avoid detection. Spacing of individuals is a behavioral trait accompanying and increasing the effectiveness of camouflage (Tinbergen *et al.* 1967; Croze 1970). Because adult Whimbrels and their exposed eggs are relatively large, flights to and from feeding areas (often off their territories) would reveal the location of closely spaced nests to predators. The wide spacing of Whimbrel nests may reduce nest predation and is likely achieved through competition for mates and territorial behavior early in the nesting season (facilitated by the *whining call*; Skeel 1978). The distance between nests is probably a compromise between selection for dispersion (detection is reduced) and for nesting close to conspecifics (joint defense is enhanced).

Philopatry

The average estimated return rate of 99% for adult Whimbrels to the hummock–bog habitat is only an approximation. Nevertheless, it strongly indicates that a high proportion return to breed there (and maintain all or part of their previous territory), that the population is stable, and that longevity is high. The longevity record is at least 11 years (Skeel 1976*b*).

In contrast, the markedly lower estimated return rate of 26% to sedge–meadow and heath–tundra habitats indicates less stability there. Movement to new areas probably accounted for much of the lower return rate. As has been found in studies of other species (Harvey *et al.* 1979; Greenwood 1980), breeding dispersal in Whimbrels may be influenced by reproductive performance the previous year. Thus, more frequent dispersal would be expected in habitats with low nesting success. Possibly dispersal is female biased, as is predominant in birds (Greenwood 1980), since two females moved over 5 km to the hummock–bog habitat.

Alternatively, or in conjunction with the above, poorer quality birds with a higher mortality rate may be relegated to the less preferred areas (see Coulson 1968). Predation on adults in the study area did not appear to greatly affect return rates in the different habitats.

Population density level

The nesting strategy of the Whimbrel is similar to Brown's (1969*a*) population density level 2. For level 2, the preferred nesting habitat is sufficiently crowded so that some individuals are forced to breed in poorer habitats. Characteristics of individuals occupying poorer habitats include a lower breeding density, a less stable population, a lower food supply, and later occupation (e.g., Kluyver and Tinbergen 1953; Glas 1960; Carrick 1963). Nesting success can vary from similar for different habitats (Kluyver and Tinbergen 1953) to rare in poor and high in preferred habitats (Carrick 1963).

For the Whimbrel population I studied, nesting success, densities, and adult return rates were lower in the poorer habitats. Although a high food supply is often characteristic of preferred habitat, this is not likely critical to the Whimbrel. Chicks are precocial and can be led to good feeding areas soon after hatching. The population density was a situation of "optimum mix" (Brown 1969*b*), for although nesting density and success differed among habitats, overall productivity was maximized because of some successful breeding in poorer habitats.

Nest-site selection

Several parameters were important in nest-site selection, with the greatest potential for more favorable sites found in the hummock–bog habitat. Density of shrubs was highest there. As well as providing wind protection, a nearby shrub would have a disruptive effect, as discussed earlier, and likely render a nest less conspicuous to predators. In hummock–bog and sedge–meadow habitats, the greater vegetation cover around nest sites than random sites likely aids in camouflage of the cryptic eggs. Almost complete cover, as found in heath–tundra habitats, is not necessarily optimal since advantages of a disruptive effect are diminished.

Nests were usually on hummocks in the low lying hummock–bog and sedge–meadow habitats. When nesting begins, these habits are wet because of snow melt and poor drainage. (The heath–tundra habitat is higher and drier.) Hummocks keep the eggs on dry ground, particularly in the hummock–bog habitat where hummocks are substantially taller. Nests were often on the lee side of large hummocks or shrubs and were thus afforded protection from the prevailing cold N to E winds that originate on Hudson Bay. Possibly Whimbrels would seek shelter from these winds, even if they were comparatively infrequent. Some nests, particularly in the hummock–bog habitat, might also have benefitted from more distant wind obstructions, such as trees, high hummocks, and shrubs. Several *Zonotrichia* species nesting in the Churchill area also select sites with wind protection (Rees 1973).

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BONGIORNO, S. F. 1970. Nest-site selection by adult Laughing Gulls (*Larus atricilla*). Anim. Behav. **18**: 434–444.

BROWN, J. L. 1969*a*. Territorial behavior and population regulation in birds. Wilson Bull. **76**: 160–169.

——— 1969*b*. The buffer effect and productivity in tit populations. Am. Nat. **103**: 329–347.

CARRICK, R. 1963. Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. *In* Proc. 13th Int. Ornithol. Congr. pp. 740–753.

CLARK, P. J., and F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, **35**: 445–453.

COULSON, J. C. 1968. Differences in the quality of birds nesting in the center and on the edges of a colony. Nature (London), **217**: 478 and 479.

CROZE, H. 1970. Searching image in Carrion Crows. Z. Tierpsychol. **5**: 1–86.

GLAS, P. 1960. Factors governing density in the Chaffinch (*Fringilla coelebs*) in different types of wood. Arch. Neerl. Zool. **13**: 466–472.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**: 1140–1162.

HADLEY, N. F. 1969. Microenvironmental factors influencing the nesting sites of some subalpine fringillid birds of Colorado. Arct. Alp. Res. **1**: 121–126.

HARVEY, P. H., P. J. GREENWOOD, and C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). J. Anim. Ecol. **48**: 305–313.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk, **96**: 651–661.

KLUYVER, H. N., and L. TINBERGEN. 1953. Territory and the regulation of density in titmice. Arch. Neerl. Zool. **10**: 265–289.

MACLEAN, G. L., and V. C. MORAN. 1965. The choice of nest site in the White-fronted Plover (*Charadrius marginatus*). Ostrich, **36**: 63–72.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. **73**: 255–261.

——— 1975. Suggestions for calculating nest success. Wilson Bull. **87**: 456–466.

NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. Ecol. Monogr. **42**: 234–269.

REES, W. E. 1973. Comparative ecology of three sympatric sparrows of the genus *Zonotrichia*. Ph.D. thesis, University of Toronto, Toronto.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. No. 191.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. **9**: 1–48.

RITCHIE, J. C. 1956. The native plants of Churchill, Manitoba. Can. J. Bot. **34**: 296–320.

ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelius phoeniceus*). I. Nesting success in marsh and upland habitat. Can. J. Zool. **50**: 247–263.

SCHAEFER, V. H. 1976. Geographic variation in the placement and structure of oriole nests. Condor, **78**: 443–448.

SCOGGAN, H. J. 1959. The native flora of Churchill, Manitoba, with notes of the history, geology, and climate of the area. National Museums of Canada and Department of Northern Affairs and Natural Resources, Ottawa.

SKEEL, M. A. 1976*a*. Nesting strategies and other aspects of the breeding biology of the Whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. M.Sc. thesis, University of Toronto, Toronto.

——— 1976*b*. Longevity record for the Whimbrel. Bird-banding, **47**: 74.

——— 1978. Vocalizations of the Whimbrel on its breeding grounds. Condor, **80**: 194–202.

——— 1982. Sex determination of adult Whimbrels. J. Field Ornithol. **53**: 414–416.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

TINBERGEN, N., M. IMPEKOVEN, and D. FRANCK. 1967. An experiment on spacing-out as a defence against predation. Behavior, **28**: 307–321.

VERHEYEN, R. 1969. Le choix du nichoir chez l'Etourneau, *Sturnus v. vulgaris* L. Gerfaut, **59**: 239–259.

ZIMMERMAN, J. L. 1982. Nesting success of Dickcissels (*Spiza americana*) in preferred and less preferred habitats. Auk, **99**: 292–298.