The Auk 109(3):601–608, 1992

ANTIPREDATOR BEHAVIOR AND BREEDING ASSOCIATIONS OF BAR-TAILED GODWITS AND WHIMBRELS

TORE LARSEN AND JOSTEIN MOLDSVOR

Department of Animal Ecology, Zoological Museum, University of Bergen, N-5007 Bergen, Norway

ABSTRACT.—Breeding associations between Whimbrels (*Numenius phaeopus*) and Bar-tailed Godwits (*Limosa lapponica*) were studied in Finnmark, northern Norway. Bar-tailed Godwit nests were distributed closer than expected by chance to Whimbrel nests. Timing of egg laying showed that the godwit, not the Whimbrel, chose to nest close to the other species. Whimbrels defended their nests aggressively against predators, while Bar-tailed Godwits did not. Godwits nested within the aggressive response distance of nesting Whimbrels. We suggest that Bar-tailed Godwits seek nest protection by breeding under the "protective umbrella" of the Whimbrel. *Received 28 May 1991, accepted 22 February 1992.*

THERE ARE numerous studies of antipredator behavior in the Charadriiformes (shorebirds and allies). A number of species in this group defend their broods actively against potential predators (Gochfeld 1984). This defense may take the form of physical attacks, and often results in the retreat of the predator. Aggressive antipredator behavior of this kind may benefit more timid species nesting in the neighborhood, and lead to breeding associations in the area defended by the aggressive species (denoted "protective umbrella" by Dyrcz et al. 1981). Well-known examples are a number of species seeking protection in colonies of terns and gulls (Koskimies 1957, Fuchs 1977, Nuechterlein 1981, Burger 1984), but even the protective umbrella of more solitary species like Lapwings (*Vanellus vanellus*; Göransson et al. 1975, Elliot 1985), Black-tailed Godwits (*Limosa limosa*; Lind 1961, Dyrcz et al. 1981), and Merlins (*Falco columbarius*; Wiklund 1982) is utilized by other species.

Breeding associations of two species may, as far as nest protection is concerned, benefit: (1) both species; (2) only one of the species; or (3) neither. The species' combined vigilance, aggressive predator responses, and/or distraction displays are the basis for both species benefitting. However, warning calls, aggressive behavior and other conspicuous displays may increase the probability of detection and, therefore, are potentially costly. Accordingly, many birds protect their nests by behaving cryptically. By breeding near species with conspicuous antipredator behaviors, a cryptically behaving species may benefit from both strategies without sharing the costs. Thus, only a single species would benefit. Factors other than nest protection (e.g. distribution of suitable nest habitats) also may cause the species to breed near each other, but with neither species benefitting.

To study the importance of behavior as opposed to habitat physiognomy in the molding of breeding associations, we studied Whimbrels (*Numenius phaeopus*) and Bar-tailed Godwits (*Limosa lapponica*) on their breeding grounds in northern Norway. Whimbrels aggressively drive potential predators off their nesting territory (Skeel 1983), and the godwit has been presumed to exploit this behavior by nesting near Whimbrels (Dransfeld 1986). Bar-tailed Godwits have been little studied on their breeding grounds (Cramp and Simmons 1983). Published accounts of the species have reported aggressive nest defense in some cases (Maher 1974, Kondratev 1982) and none in another case (Dransfeld 1986). We found a breeding association between Bar-tailed Godwits and Whimbrels, and discuss their nest spacing in relation to nesting habitat, phenology and antipredator behavior.

STUDY AREA AND METHODS

Field studies were performed in 1987 (13 May to 19 July), 1989 (15 May to 28 June) and 1990 (11 to 25 June) in a 14 km^2 area near Kautokeino, Norway (69°N, 24°E). The area is a mosaic of palsa bogs (wet bogs with dry ridges raised by a core of permanent ice) with shallow lakes and ponds, and dry, lichen-covered morains with open birch (*Betula* sp.) forests. Altitude is between 375 and 440 m (a.s.l.). Human presence is restricted to the winter season, when herds of reindeer (*Rangifer tarandus*) are brought into the area.

Nest distribution.—To determine the distribution of habitat types in the study area, we drew a grid of

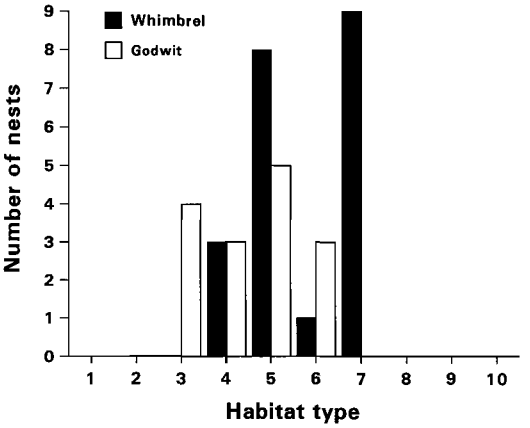

Fig. 1. Nest habitats used by Whimbrels and Bar-tailed Godwits. Nest habitats 1–7 are ordered by degree of wetness. Habitat types (percent of total study area given in parentheses): (1) open water (5.2); (2) wet cotton-grass bog (5.4); (3) humid cotton-grass bog (5.7); (4) broken, scrubby peat bog (9.3); (5) flat palsa bog with crowberry and open dwarf birch cover (17.1); (6) rich lichen-dominated heath (10.1); (7) poor lichen-dominated heath (12.4); (8) dwarf birch scrub (7.8); (9) open birch forest (13.0); (10) dense birch forest (14.0).

squares 200 × 200 m on a map, resulting in 386 points regularly distributed over the study area. The points were investigated in the field and classified according to vegetation type. Ten different habitat types were recognized (see Fig. 1). Godwit and Whimbrel nests in the study area were classified according to these habitat types.

Nests were censused by recording territorial behavior and, subsequently, observing the different pairs from vantage points. The different parts of the study area were censused systematically every second day. When located, nests were plotted on aerial photographs (scale 1:25,000) in order to establish nest distances (accuracy ca. ±10 m). Distances between nests were measured from the photographs with calipers (precision 0.05 mm).

To find out whether nests of the two species were distributed nonrandomly relative to each other, a number of points corresponding to the number of godwit nests were spread randomly on the photographs. This was done by assigning consecutive numbers to the 386 points from the grid described above, loading these in a calculator and drawing them by a random-number function. Because no godwit nest was placed more than 50 m from marsh areas, points outside this limit were excluded, and all random points were finally situated in potential nest habitats. Distances from these random points to the nearest Whimbrel nest were measured as above. A Mann-Whitney *U*-test was employed to test the distribution of the random points relative to actual godwit nests. This simulation was repeated 10 times, and the 10 tests were finally treated in a combined probability test (Sokal and Rohlf 1981).

Agonistic behavior and antipredator behavior.—Whimbrels and godwits foraging near each other were watched for interspecific aggressions (i.e. instances where one bird caused another to flee or defend itself). Notes from observations of relevant behaviors were dictated on a tape recorder, with the distance from the observer to the birds being sufficient (usually 200–400 m) so that the birds were not affected. The maximum distance at which one of the species attacked the other was 35 m, and observations of species pairs outside of this limit were excluded from the analysis of agonistic behavior between Whimbrels and godwits.

Behavior of Whimbrels and godwits in the presence of avian predators was recorded throughout the season. Avian nest predators in the area include Common Ravens (*Corvus corax*), Hooded Crows (*Corvus corone cornix*) and Long-tailed Jaegers (*Stercorarius longicaudus*). There were only a few raptors; one pair of Rough-legged Hawks (*Buteo lagopus*) nested in the area in 1987. Although no corvids nested inside the study area, one to five individuals were usually observed daily, constituting the most important nest predators in the area. Five jaeger pairs nested in the area in 1987, and two pairs in 1989 and 1990.

When an avian predator appeared, distances were noted at which the shorebirds gave their first warning calls and launched attacks. Distances were estimated by plotting the positions of the birds on maps (scale 1:25,000). Two types of responses to avian predators were recognized: "Attack" denotes an aggressive attack against the overflying predator, resulting in physical contact and/or escape behavior of the predator. "Warning call" means that warning calls were given by birds on the ground or circling the predator, without attacks being launched. "No response" is used when the bird remained silent on the ground. Only observations within the maximum response distances were used in the calculations, thus excluding cases where the predator appeared too far away to evoke any response at all.

Before egg laying, the response distance is defined as the distance between predator and bird at first response, whereas after egg laying it is defined as the distance between predator and nest or chicks.

Red foxes (*Vulpes vulpes*) and ermines (*Mustela erminea*) were the only ground predators observed in the study area. A Whimbrel was observed once to dive within 1.5 m of a fox that was 10 m from the nest. Because sightings were few, we studied the responses of Whimbrels and godwits to our own intrusions in the nest areas. The responses of waders to man generally resemble those elicited by other ground predators (Armstrong 1956, Gochfeld 1984). We approached the birds, nests or chicks directly at a steady pace and were clearly visible to the birds. Visits were

divided evenly among the pairs, to avoid habituation to the observer. The same nest was visited no more than eight times (average of five).

Laying dates and breeding success.—Most Whimbrel nests were found during egg laying. Godwit nests were more difficult to locate, and none was found before the clutches had been completed. Where dates of egg laying had to be estimated by counting back from the hatching date, an incubation period of 21 days was used for Bar-tailed Godwits (Haftorn 1971, Cramp and Simmons 1983) and 25 days for Whimbrels (pers. observ.).

Both species escorted their chicks several kilometers away from the nest area within a week after hatching. Therefore, we have no data on chick survival until fledging, but measure breeding success as number of nests not predated before hatching. Mayfield's (1975) method is used to estimate nest success. Average survival rate (S) is expressed as

$$S = (1 - P)^n, \quad (1)$$

where P is mortality rate per observed nest-day and n is incubation period in days.

Results

Nest habitats and nest distribution.—We found 21 Whimbrel nests and 15 godwit nests in the study area during the three seasons of study. Palsa bogs with open dwarf birch (*Betula nana*) cover (medium wetness) were used as nest habitats by both species (Fig. 1). Poor lichen heath (dry) was used exclusively by the Whimbrel, and cotton-grass (*Eriophorum*) bogs (wet) exclusively by the Bar-tailed Godwit. Wetness was classified by measuring how deep a 2.7 kg rod sank into the ground. Pooling the nests and ranking the nest habitats by degree of wetness showed that the godwit selected wetter nest habitats than the Whimbrel (Mann-Whitney U-test, $U = 66.5$, $n_1 = 21$, $n_2 = 15$, $P < 0.02$).

In 1990, the study area was not examined before the middle of the incubation period. Because of heavy nest predation (see section on breeding success), many Whimbrel nests were probably already predated and, consequently, never located. Nests found in 1990, therefore, are not included in the calculations on nest distribution. In 1987 and 1989, 16 Whimbrel nests and 12 godwit nests were found in the study area. These include a nest scrape actively defended by a Whimbrel pair, but abandoned or predated around egg-laying, two Whimbrel nests and one godwit nest already predated when found, and four godwit nests that were located immediately after hatching. Based on presence, territorial behavior, and antipredator responses of birds of the two species throughout the season, we assume that we found most or all nests in the area. Six of the 16 Whimbrel nests had no godwit neighbor.

TABLE 1. Nearest intra- and interspecific distances between Whimbrel and godwit nests.[a]

	Mean	SD	Range	n
Godwit-Whimbrel	245[b]	112	135–430	11
	305[c]	214	135–920	12
Godwit-godwit	760	325	110–1,050	12
Whimbrel-godwit	505	420	135–1,560	16
Whimbrel-Whimbrel	845	395	475–1,990	16

[a] Number of Whimbrel nests and number of godwit nests were not identical. Some godwit nests, therefore, were used more than once in calculating Whimbrel-godwit distances.

[b] Excluding one outlier.

[c] Including a godwit nest placed 100 m from a Long-tailed Jaeger nest, but 920 m from nearest Whimbrel.

Mean nearest-nest distances between Bar-tailed Godwits and Whimbrels were significantly shorter than nearest intraspecific nest distances for both species (Table 1; Bar-tailed Godwit, $U = 30$, $n_1 = n_2 = 12$, $P < 0.02$; Whimbrel, $U = 53$, $n_1 = n_2 = 16$, $P < 0.02$). The combined probability test of nest distribution on suitable nest habitats in the study area (Table 2) showed that godwit nests were closer to Whimbrel nests than would be expected if they were randomly distributed (1987, $P < 0.01$; 1989, $P < 0.001$). Cotton-grass bogs and dry lichen heath, favored respectively by godwits and

TABLE 2. Monte Carlo simulation of nearest-neighbor distance between random points and Whimbrel nests compared to godwit-Whimbrel distances.[a]

	Year	
Simulation	1987 (7 godwit nests)	1989 (4 godwit nests)
1	0.054	0.028
2	0.164	0.114
3	0.022	0.028
4	0.072	0.058
5	0.534	0.028
6	0.208	0.028
7	0.026	0.028
8	0.260	0.028
9	0.456	0.028
10	0.164	0.028
$-2\Sigma \ln P$	41.926	67.247
	$P < 0.01$	$P < 0.001$

[a] Mann-Whitney U-test probabilities that shorter distance between godwit nests and Whimbrel nests, compared to random points and Whimbrel nests, could have arisen by chance. Statistics for combined probability test given at bottom.

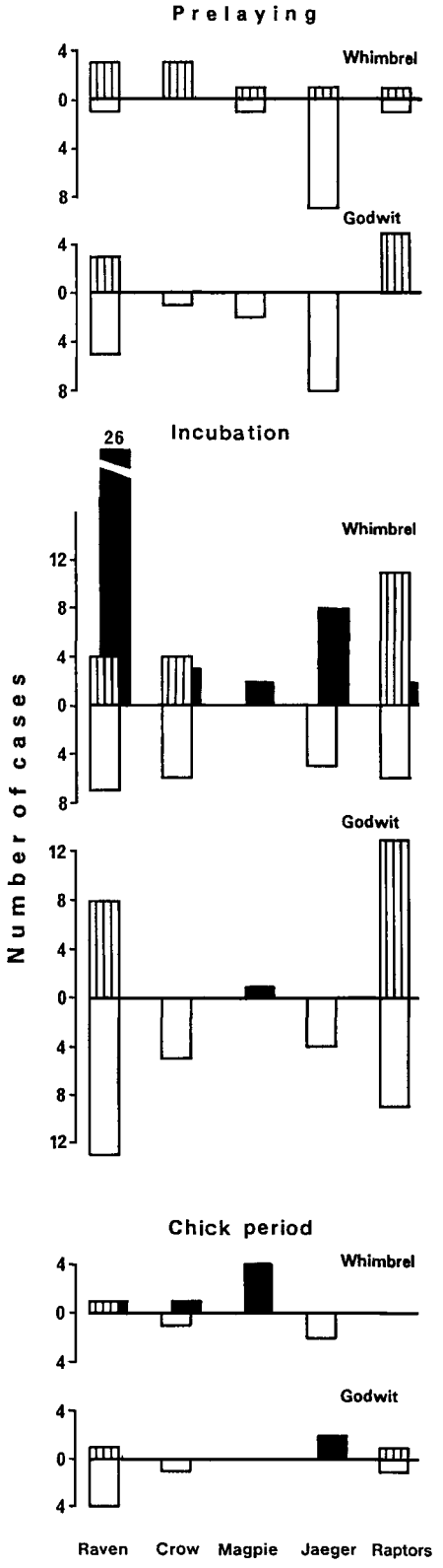

TABLE 3. Number of observations of interspecific behavior between Whimbrels and Bar-tailed Godwits.[a]

	Prelaying	Incubation	Chick period	Total
Whimbrel attacks	16	4	0	20
Godwit attacks	0	0	0	0
No aggression	18	12	2	32
Total	34	16	2	52

[a] Maximum response (attack) distance was 35 m. Observations outside this limit not included. Periods of breeding season are defined individually for each pair. Prelaying includes the period from arrival in study area until laying of first egg in each clutch, while incubation extends from then until hatching.

Whimbrels, were not found closer to each other than expected at random.

Agonistic and antipredator behavior.—Aggressive behavior between Whimbrels and godwits was recorded significantly more often in the prelaying period than in both the incubation period (Table 3; chi-square test, $X^2 = 18.26$, df $= 1$, $P < 0.001$) and the chick period ($X^2 = 8.6$, df $= 1$, $P < 0.01$). There was no difference between the incubation and chick periods. Foraging birds of the two species within 35 m of each other (maximum agonistic response distance) were recorded 52 times. Aggressive behavior was observed on 20 occasions, all of them with the Whimbrel as the aggressor. Observations were done on six different feeding areas over two years to achieve independent observations. To get an indication of whether aggression was due primarily to food competition or spacing of nests, the distance to nearest Whimbrel nest was measured for all aggressive interactions recorded before godwits started egg laying. Distances were ranked, and a significant relation was found between aggressive behavior and short distance to Whimbrel nests ($U = 158$, $n_1 = 13$, $n_2 = 14$, $P = 0.0006$). Before Whimbrels started egg laying, aggression may have been due to food competition (Larsen in prep.).

The behavior of 12 Whimbrel pairs and 9 Bar-tailed Godwit pairs in the presence of avian predators was recorded on 115 and 87 occasions, respectively (Fig. 2). Whimbrels attacked po-

←

Fig. 2. Behavior of Whimbrels and Bar-tailed Godwits in presence of avian predators within maximum attack distance of the Whimbrel (500 m). Number of attacks (black bars), warning calls (hatched bars), and no responses (open bars) given for Whimbrels and godwits in each of the three periods of breeding season (defined in Table 3).

tential predators 47 times and the godwits 3 times. Whimbrels from all 12 pairs were observed attacking at least three times. The total numbers found by pooling all species of nest predators show that Whimbrels are significantly more aggressive than godwits ($X^2 = 40.75$, df $= 2$, $P < 0.001$).

The antipredator behavior of the species changed between the different periods of the breeding cycle. During the prelaying period, none of the species attacked avian predators. The difference in antipredator behavior of the two species was most clear in the incubation period, when the Whimbrel attacked predators significantly more often than the godwit ($X^2 = 35.87$, df $= 2$, $P < 0.001$). When the "off-duty" Whimbrel was present near the nest territory (i.e. within 400 to 500 m of nest) and able to respond to avian predators, the incubating Whimbrel remained silent on the nest in 16 of 27 cases where the identity of the responding bird could be ascertained. Only during egg laying did it accompany the off-duty bird in attacks ($n = 4$). When the off-duty Whimbrel was not present in the neighborhood, the incubating bird attacked ($n = 2$) or gave warning calls ($n = 2$). The incubating godwit gave warning calls on 2 out of 11 occasions when the off-duty bird was present, and never attacked. Also in this species, the off-duty bird usually stayed within 400 to 500 m of the nest.

After hatching, the pairs left the nest area with their chicks and were difficult to localize. Accordingly, we have only a few observations of family groups with overflying avian predators. In 10 cases, the Bar-tailed Godwit attacked predators (Long-tailed Jaegers) twice, while the Whimbrel attacked avian predators in 6 of 10 encounters.

The Common Raven is probably the most important nest predator in the area. The Whimbrel attacked ravens in 27 of 42 instances where this species was observed within the maximum attack distance (Fig. 2). The mean attack distance was 205 m ($n = 20$, range 60–500, SD $= 128$). The Bar-tailed Godwit gave warning calls at the presence of ravens on 12 occasions and remained silent on 22. Whimbrels responded significantly more often towards ravens than did godwits ($X^2 = 26.76$, df $= 2$, $P < 0.001$).

The response to avian predators (all species) in their common nest area was recorded for Whimbrels and godwits simultaneously on 34 occasions. The Whimbrel attacked the predator 17 times, 4 of which were accompanied by warning calls from its godwit neighbor. The associated Bar-tailed Godwit never attacked the predator. Totally, the godwit remained silent on 23 occasions and gave warning calls on 11. The Whimbrels responded significantly more often to predators than did their associated godwit neighbors ($X^2 = 29.96$, df $= 2$, $P < 0.001$).

There was no significant relationship between avian antipredator strategies of godwits and the distance to nearest unpredated Whimbrel nest, nor any relation between type of behavior and the presence or absence of a Whimbrel neighbor. However, data are limited for many of the nests.

Responses to the approach of a human observer are summarized in Tables 4 and 5. In the prelaying period, both species gave warning calls and took flight at a distance. The Whimbrel was flushed at significantly longer distances (94 m, SD $= 50$, $n = 10$) than the godwit (37 m, SD $= 32$, $n = 20$) in the same habitat types ($U = 16.5$, $n_1 = 20$, $n_2 = 10$, $P < 0.02$). Single birds of both species did not respond differently from birds in pairs.

During incubation, off-duty birds of both species gave warning calls whenever the observer was detected. Incubating Whimbrels responded by leaving the nest early when approached. The Bar-tailed Godwit generally sat tight, leaving the nest at short range by means of an explosive departure. The nest departure distances are significantly different between the species in the

TABLE 4. Mean distances to Whimbrel and Bar-tailed Godwit nests at which an observer became visible, and departure distances for incubating birds. Distances in meters with sample sizes (n) in parentheses.

		Off-duty bird	
	Observer visible	Present	Not present
Whimbrel	300 (18)	110 (10)	70 (8)
Godwit	225 (30)	12 (14)	10 (16)

TABLE 5. Mean distances to Whimbrel and Bar-tailed Godwit broods at which an observer became visible to parents, and parents' response distances. Distances in meters with sample sizes in parentheses.

	Observer visible	Warning call	Flight
Whimbrel	300 (18)	250 (18)	250 (18)
Godwit	300 (18)	250 (18)	120 (13)

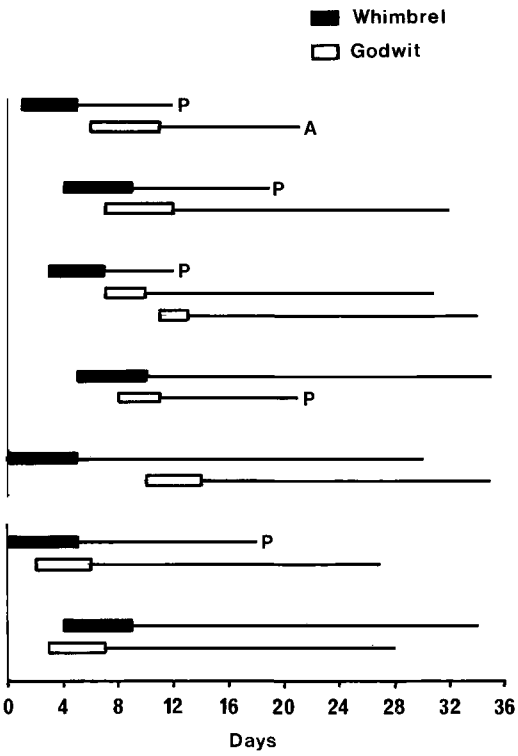

Fig. 3. Nest histories of associated Whimbrel and godwit neighbor pairs in study area in 1987 (upper five groups; day 0 = 25 May) and 1989 (lower two; day 0 = 24 May). Data given for nests where laying dates could be accurately determined. Boxes indicate the egg-laying period and lines the incubation period. Letters indicate approximate date of predation (P) and nest abandonment (A).

incubation period (Table 4; $U = 91.5$, $n_1 = 18$, $n_2 = 30$, $P = 0.0002$). The departure distance of the Whimbrel is positively correlated with the distance at which the observer became visible ($n = 25$, $Y = 34.3 + 0.252X$, $r = 0.559$, $P < 0.01$). For the godwit there is no such correlation. Incubating Whimbrels left their nests at significantly longer distances when the off-duty bird was present in the area than when it was not ($U = 12.5$, $n_1 = 8$, $n_2 = 10$, $P < 0.05$). The presence of the off-duty bird did not influence the departure distance of the godwits.

In the chick period, there were no significant differences in response distances between Whimbrels and godwits. Both species gave warning calls at long distances (i.e. at several hundred meters, Table 5) and took flight to meet the intruder. Whimbrels and Bar-tailed Godwits spaced out after hatching, and no type of association was observed in the chick period.

Laying dates and breeding success.—Bar-tailed Godwits and Whimbrels arrived at the study area simultaneously. Some of the godwits were paired upon arrival, while the first Whimbrel pairs were observed four days after arrival.

Because of nest predation, one godwit nest and three Whimbrel nests could not be accurately dated. Figure 3 presents data on Whimbrel-godwit neighbor groups where laying dates could be determined. In all groups except one, godwits started egg laying after the associated Whimbrel pair (i.e. two to nine days later). Ranking the nests by relative age shows that godwits started egg laying significantly later than their Whimbrel neighbors (Wilcoxon matched-pairs test; $z = 2.38$, $n = 8$, $P = 0.016$). Laying dates for godwits are estimates based on an incubation period of 21 days as stated in the literature. There is a tendency even when the incubation period is set to 23 days ($z = 1.75$, $n = 8$, $P = 0.076$).

Whimbrels had 13 out of 20 nests predated, and hatched 25 of 73 eggs (34%). Three of the 15 godwit nests were lost to predators. In addition, one godwit nest was deserted, and 38 of 53 eggs hatched (72%). There was no significant year-to-year variation in egg predation for any of the species.

By Mayfield's (1975) method, the probability of nest survival is 11% for the Whimbrel and 46% for the godwit. Predation rates are significantly higher for the Whimbrel than for the godwit ($X^2 = 5.46$, df = 1, $P < 0.02$). Predation on Whimbrel nests with an associated godwit nest was not significantly different from predation on solitary Whimbrel nests.

DISCUSSION

To demonstrate the presence of a "protective-umbrella association" between two species, at least three requirements have to be fulfilled: First, the umbrella species must perform the more aggressive antipredator behavior. Second, the associating species must place its nest within the area defended by the umbrella species. Third, the umbrella species should establish its nest territory before the associating species. The last requirement is a necessary condition for the second. If these three conditions are not fulfilled, what may seem to be an active association between two species may simply be a coincidental byproduct of similar demands for nest habitats. Finally, to establish whether an asso-

ciation really functions as a protective umbrella, a test should be done of nest predation inside and outside the area protected by the umbrella species. Due to the lack of unassociated godwits, this test could not be done on the birds in our study area. Within the Norwegian breeding distribution of the Bar-tailed Godwit, we still have not found a population of any size without breeding Whimbrels. Our discussion, therefore, will focus on how the data fit the first three requirements listed above, to decide whether the godwit/Whimbrel association is of the protective-umbrella type.

The antipredator strategies of Whimbrels and godwits clearly are different. The Whimbrel is an aggressive nest defender, attacking avian predators within a radius of 500 m from the nest. It also responds early to intrusions from observers. The Bar-tailed Godwit, on the other hand, does not attack avian predators during incubation (even after predation of the associated Whimbrel nest) and relies on a cryptic strategy towards ground predators. These differences are highly significant and fit the first requirement. A further confirmation of a possible protective-umbrella relation between the two species is given by the different responses of associated Whimbrels and godwits to predators entering their common nest area. The Whimbrel attacked, while the godwit remained silent, in more than two-thirds of the cases.

Godwit nests were placed closer to Whimbrel nests than would be expected if they were randomly distributed on suitable habitats. In fact, the second requirement is met by 11 of 12 godwit nests placed within maximum attack distance of the Whimbrel. Mean attack distance towards corvids (205 m) is only slightly shorter than mean interspecific nest distance (245 m). One of the godwit nests was placed 100 m from the nest of a Long-tailed Jaeger, another species featuring aggressive nest defense. Predator attack distances of Whimbrels were highly variable. This is probably caused by reduced detectability of approaching avian predators in certain sectors around the Whimbrel nests, due to trees and ridges. All godwit nests except one were placed free of such obstacles between them and their Whimbrel neighbor, but this may be a result of preferences for open nest habitats.

The third requirement is that the associating species should postpone egg laying until the umbrella species has chosen a nest site or started egg laying. During the spring thaw on Finnmarksvidda, snow melting starts in the wet parts of the bogs. Consequently, nest habitats preferred by the Bar-tailed Godwit are free of snow first. However, although Whimbrels and godwits arrived at the nesting area simultaneously, godwits started egg laying after their Whimbrel neighbors. The date of territory establishment rather than date of egg laying perhaps is the most appropriate measure in this case, and may explain the fact that one of the godwit pairs started egg laying before the nearest Whimbrel pair. The date of territory establishment, however, is difficult to quantify.

Our data suggest that the Whimbrel/Bar-tailed Godwit association on Finnmarksvidda is an example of an actively exploited protective umbrella, rendered by the aggressive Whimbrel and exploited by the cryptic godwit. A puzzling fact is the heavy predation on Whimbrel nests found in 1987, 1989, and 1990. Predation removed the protection rendered by Whimbrels in most species pairs, without adverse effects on the hatching success of the godwits. However, this does not imply that the protective umbrella is unimportant to the godwits. We suggest that the umbrella effect is most important to the godwits during egg laying and the early phases of the incubation period. Around egg laying, the pair performs conspicuous nest-site-selection behavior (Byrkjedal et al. 1989), and spends much time in the nest area. Before completion of the clutch, eggs are brooded only irregularly. Lind (1961) found that egg losses in the Black-tailed Godwit were disproportionately high early in the egg-laying phase, even though this species is an aggressive nest defender. After completion of the clutch, the incubating Bar-tailed Godwit is extremely cryptic, and an aggressive neighbor is presumably no longer very important.

Whimbrels defend large territories against conspecifics (Skeel 1983). This may be an adaptation to counteract density-dependent nest predation. Colonial breeding is usually regarded as advantageous with respect to avian predators (Wiklund 1982, Elliot 1985), but for a ground-nesting bird this strategy may increase vulnerability to ground predators. Even large, aggressive birds like Whimbrels and Long-tailed Jaegers cannot defend their nest from large ground predators like foxes (pers. observ.). Spacing out nests is a way of counteracting predation from ground predators (Tinbergen et al. 1967). A consequence of this strategy would be

to expel other birds trying to nest in the vicinity of the nest site. Our observations of agonistic behavior between Whimbrels and godwits support this theory, since aggression was directed from Whimbrels to godwits, and depended on the distance to the nearest Whimbrel nest. Furthermore, aggression was most frequent in the period before the godwits had established a nest territory, or at least started egg laying. Aggressive behavior from Whimbrels may explain why interspecific nest distances are relatively long.

Based on data for laying dates, nest spacing and antipredator behavior of Whimbrels and godwits, we suggest that this is a nesting association exemplifying the protective-umbrella effect. This influences the spatial distribution of the Bar-tailed Godwit on its breeding grounds.

ACKNOWLEDGMENTS

We are most grateful to Ingvar Byrkjedal (Museum of Zoology, University of Bergen) for his numerous ideas and suggestions, and his help with the field work in 1987. Göran Högstedt (also of the Museum) has contributed with advice on statistical treatment of the data, while Michael Gochfeld provided improving comments to the manuscript. Bjørn Larsen assisted invaluably in the field in 1989, and Ole H. Gaino and Johan J. Gaup provided transport and lodging in the study area.

LITERATURE CITED

ARMSTRONG, E. A. 1956. Distraction display and the human predator. Ibis 98:641-655.

BURGER, J. 1984. Grebes nesting in gull colonies: Protective associations and early warning. Am. Nat. 123:327-337.

BYRKJEDAL, I., T. LARSEN, AND J. MOLDSVOR. 1989. Sexual and antagonistic behaviour of Bar-tailed Godwits on the breeding grounds. Ornis Scand. 20:169-175.

CRAMP, S., AND K. E. L. SIMMONS. 1983. The birds of the western Palearctic, vol. 3. Oxford Univ. Press, Oxford.

DRANSFELD, H. 1986. Hekkende vadere på våtmarkene i Finnmark. Vår Fuglefauna 9:11-16.

DYRCZ, A., J. WITKOWSKI, AND J. OKULEWICZ. 1981. Nesting of "timid" waders in the vicinity of "bold" ones as an antipredator adaptation. Ibis 123:542-545.

ELLIOT, R. D. 1985. The exclusion of avian predators from aggregations of nesting Lapwings *Vanellus vanellus*. Anim. Behav. 33:308-314.

FUCHS, E. 1977. Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed gulls *Larus ridibundus* with special reference to the Sandwich tern *Sterna sandvicensis*. Ornis Scand. 8:17-32.

GOCHFELD, M. 1984. Antipredator behavior: Aggressive and distraction displays of shorebirds. Pages 289-377 *in* Behavior of marine animals. Vol. 5, Shorebirds: Breeding behavior and populations (J. Burger and B. Olla, Eds.). Plenum Press, New York.

GÖRANSSON, G., J. KARLSSON, S. G. NILSSON, AND S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: An experimental study. Oikos 26:117-120.

HAFTORN, S. 1971. Norges fugler. Universitetsforlaget, Oslo.

KONDRATEV, A. Y. 1982. Biologiya kulikov v tundrach severovostoka Azii. Izdatel'stvo "Nauka," Moscow.

KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. Ornis Fenn. 34:1-6.

LIND, H. 1961. Studies on the behaviour of the Black-tailed Godwit (*Limosa limosa* (L.)). Munkegaard, Copenhagen.

MAHER, W. J. 1974. Ecology of Pomarine, Parasitic, and Long-tailed jaegers in northern Alaska. Pacific Coast Avifauna 37:1-148.

MAYFIELD, H. F. 1975. Suggestions of calculating nest success. Wilson Bull. 87:456-466.

NUECHTERLEIN, G. L. 1981. "Information parasitism" in mixed colonies of Western Grebes and Forster's Terns. Anim. Behav. 29:985-989.

SKEEL, M. A. 1983. Nesting success, density, philopatry, and nest-site selection of the Whimbrel (*Numenius phaeopus*) in different habitats. Can. J. Zool. 61:218-225.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, San Francisco.

TINBERGEN, N., M. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defence against predators. Behaviour 28:307-321.

WIKLUND, C. G. 1982. Fieldfare *Turdus pilaris* breeding success in relation to colony size, nest position and association with Merlins *Falco columbarius*. Behav. Ecol. Sociobiol. 11:165-172.