

NESTING NEAR A COMMON TERN COLONY INCREASES AND DECREASES SPOTTED SANDPIPER NEST PREDATION

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ABSTRACT.—We identified predators of Spotted Sandpiper (*Actitis macularia*) nests before and after the establishment of a Common Tern (*Sterna hirundo*) colony on an island in north-central Minnesota. Migratory Ruddy Turnstones (*Arenaria interpres*) became major nest predators of the sandpipers after establishment of the tern colony. Turnstones feeding on tern eggs destroyed significantly more sandpiper nests near the colony than far from it. When mink (*Mustela vison*) were present they were the major nest predators of both sandpipers and terns. However, when the tern colony was present, mink predation of sandpiper nests was reduced significantly. Close proximity of sandpiper nests to those of the terns resulted in both increased and decreased predation, depending on time of year, type of predator, and chance arrivals of occasional predators. Received 19 November 1990, accepted 13 May 1991.

BIRDS that nest in colonies might gain advantages through increased vigilance, defense against predators, and information transfer about resources. On the other hand, colonial nesters might attract predators by their conspicuousness and might experience competition for local resources (for recent reviews, see Wittenberger and Hunt 1985, Krebs and Davies 1987, Siegel-Causey and Kharitonov 1990). Various species of grebes, shorebirds, and ducks have been reported to associate actively with colonial species (e.g. shorebirds—Walters 1957, Höhn 1967, Hildén and Vuolanto 1972, Göransson et al. 1975, Dyrce et al. 1981, Brearey and Hildén 1985; grebes—Nuechterlein 1981, Burger 1984; ducks—Vermeer 1968, Evans 1970, Dwernychuk and Boag 1972a, Kistchinski and Flint 1974, Götmark and Ahlund 1988, Götmark 1989). By associating with a colony, individuals might benefit from aggressive colony behavior toward predators or from the warning system of the colony (Koskimies 1957, Nuechterlein 1981). In contrast, species that associate with a colony might sometimes be subject to more predation both from attracted predators and from colony members (Dwernychuk and Boag 1972a). When association with the colony is active, increased predation (as well as increased competition, aggression, cuckoldry, and disease) is generally considered to be offset by advantages of being close to the colony.

The degree of antipredation advantage of being near a colony is not known. Further, we do not know if birds associated with a colony suffer increased nest predation. Studies of the

nesting success of noncolonial species associated with a colony usually have no comparable information on nesting success away from colonies. In the few studies that examined the same population with and without an associated colony, seasonal effects confounded colony effects. For example, Pienkowski (1984) reported a decrease in predation of Common Ringed Plover (*Charadrius hiaticula*) nests beginning in June and attributed this to an increase in alternative foods for predators and establishment of an Arctic Tern (*Sterna paradisaea*) colony. Götmark (1989) found Common Eiders (*Somateria mollissima*) that began to nest before the associated gulls (*Larus marinus*, *L. argentatus*, *L. fuscus*, and *L. canus*) established colonies, experienced increased nest predation inside the colonies during laying, and decreased nest predation inside the colonies during incubation. Later-nesting eider species showed no increased nest predation during laying (Götmark 1989).

The establishment of a colony of Common Terns (*Sterna hirundo*) at the site of a long-term Spotted Sandpiper (*Actitis macularia*) study presented a prime opportunity to compare the incidence and types of nest predation with and without the presence of the colony. Our objectives were to (1) document Spotted Sandpiper nest predators, (2) look for within-season changes in predation, (3) compare predation in years without the Common Tern colony to years when it was present, and (4) evaluate whether sandpipers were benefited or harmed by presence of a tern colony.

STUDY AREA AND METHODS

A breeding population of Spotted Sandpipers has been studied on Little Pelican Island (LPI), Leech Lake, Cass County, Minnesota (47°07'N, 94°22'W) from 1975 to 1990 (Maxson and Oring 1980, Oring and Lank 1982, Lank et al. 1985, Colwell and Oring 1989). The island is 1.6 ha and lies 7–8 km from the mainland. Its vegetation includes sandy open beaches, semi-open herbaceous areas, a cattail (*Typha latifolia*) marsh, and deciduous woods.

Numerous potential egg-eating predators are resident or transient on LPI. Ring-billed Gulls (*Larus delawarensis*) and Herring Gulls (*L. argentatus*) (Hatch 1970, Burger and Lesser 1978) come from Gull Island, 300 m to the southwest. Migratory Ruddy Turnstones (*Arenaria interpres*) (Parkes et al. 1971, Brearey and Hildén 1985) occurred in all years of the study from early May through mid-June (Oring and Maxson 1984). Common Grackles (*Quiscalus quiscula*) are also suspected egg predators and prey on Spotted Sandpiper chicks (Maxson 1977). Common Terns could also damage eggs, but we did not see evidence of this at our study site. Deer mice (*Peromyscus maniculatus*) were resident until 1978 when they were removed by trapping (Maxson and Oring 1978). Meadow voles (*Microtus pennsylvanicus*) are occasional egg predators (Maxson and Oring 1978) and remain resident. At least one mink (*Mustela vison*) was resident in 1975. In 1990 an adult and 4 juveniles were resident by 30 June. Mink have also preyed on single nests in other years. A weasel (*Mustela* sp.), believed to be a least weasel (*M. nivalis*), preyed on nests during 1-week periods in 1985 and 1987.

In 1989, Common Terns nested on LPI for the first time. Pairs (20) occupied the north beach beginning on 14 June. In 1990, terns began nesting on the north beaches by 4 June. A maximum of 126 nests at a time, and a total of approximately 150 nesting pairs, were present (Fig. 1). Terns preferred to nest in areas of open sand and debris 0–2 m from semi-open vegetation or cattails, much as described by Burger and Lesser (1978). The periphery of the tern colony was defined roughly by the beginning of semi-open vegetation, which is where Spotted Sandpipers commonly nested, regardless of tern presence (Oring et al. 1983).

We censused tern nests by methodically walking through the colony once per week (Reed et al. 1991). For each week, the minimum number of nests depredated was calculated by subtracting the number of completed nests actually counted from the number of nests that would have been expected if all one-, two- and three-egg nests of the previous week had been completed. This value is an underestimate because it excludes egg loss from incomplete clutches and ignores new nests established during the week.

We observed birds in beach and semi-open herbaceous areas, and parts of densely vegetated areas from four 3-m towers May through July each year.

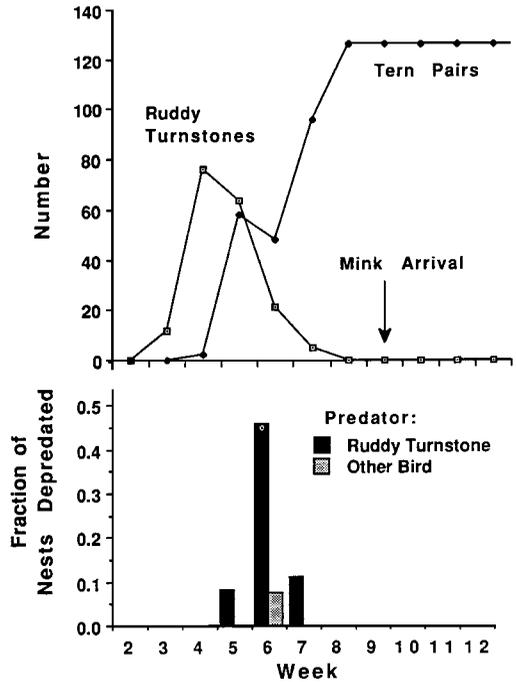


Fig. 1. Ruddy Turnstone and Common Tern abundances (top) and fraction of Spotted Sandpiper nests depredated (bottom) in 1990. Turnstone abundance is reported as maximum number seen in one day during the week; tern pairs are maximum number observed at weekly census. Week 2 is 8–14 May.

Observations were generally for 3-h periods in the morning and evening. Except for brief periods as we went to the towers and occasional periods of netting Spotted Sandpipers, our presence was not disruptive to tern colony or sandpipers. Mist-netting activities occasionally disturbed portions of the colony or individual sandpipers but did not engender nest depredations. The location, clutch initiation date, and fate of most sandpiper nests were known.

Once a clutch was initiated, we checked the nest regularly to determine if it was intact. If eggs were missing, the date was recorded and the identity of the predator was determined when possible by examination of nest remnants. Ruddy Turnstones consumed sandpiper eggs in the same manner as reported for tern eggs (Bent 1929, Parkes et al. 1971, Brearey and Hildén 1985; but see Crossin and Huber 1970, Loftin and Sutton 1979). They generally punctured the egg, cracked it open, and consumed its contents. Depredation by grackles or turnstones was presumed if shells remained in the nest area. Turnstone and grackle activity could sometimes be distinguished by observations of which predator had been recently present in the area. Mouse predation was indicated by damage to single eggs, mouse droppings, and egg scratches or punctures (Maxson and Oring 1978). Be-

cause mice were trapped and removed in some years, and have caused relatively little nest damage since, nests predated by mice were excluded in further analyses. Minks were indicated by scats, scent, and the sudden disappearance of complete nests.

Because depredation by Ruddy Turnstones was observed early in the season and mink depredation later in the season, nesting-success data were divided into nests initiated before 10 June and nests initiated after 10 June. This date was chosen because in all years the majority of Ruddy Turnstones had departed by 10 June, and no mink had dispersed to LPI by this date. Sample size for Fisher's exact test was increased by including nests with unknown clutch-initiation date but with nest destruction date before 10 June. Before any analysis of predation data, nests were also classified as near or far from the tern colony. A nest was considered *near* if an observer at the sandpiper nest elicited nest defense responses from nearby terns. All nests classified as near were within 3 m of a tern nest. There were no cases where this criterion was ambiguous.

A *successful nest* was one in which at least one egg hatched. Only nests in which all eggs were destroyed were included in depredation analyses.

RESULTS

Predation on tern nests.—Of the potential egg-predators on Little Pelican Island (LPI), only Herring Gulls and Ruddy Turnstones were observed to damage and consume Common Tern eggs. Herring Gulls removed one egg at a time and consumed them away from the colony. Turnstones are known to capitalize on human disturbance to gain access to nests (Bent 1929, Crossin and Huber 1970, Parkes et al. 1971) and, in our study, twice destroyed second and third eggs of a tern clutch while the parent was disposing of the shell of a previously consumed egg. Turnstones destroyed a minimum of 27 tern nests. We observed Common Terns reacting aggressively to Herring Gulls (see also Erwin 1979), but not turnstones or grackles during the incubation period. Turnstones were tolerated among tern nests and sometimes poked at eggs underneath an incubating adult. After eggs hatched, terns were strongly aggressive toward humans and other tern chicks (Erwin 1988). The qualitative increase in aggression we observed during brooding is consistent with quantitative results of Erwin (1979). Turnstones departed before terns began to hatch.

Arrival of a mink family in 1990 led to sudden large-scale disappearance of tern eggs and chicks. A minimum of 29 tern nests were destroyed in the first week mink were present (Reed et al.

1991). Approximately 50 tern chicks were left in the colony on 30 July, ca. 10% of the number of eggs laid. Mink activity was crepuscular or nocturnal. When the tern colony was on Gull Island, terns were once observed mobbing a mink, so we assume they responded similarly to mink on LPI.

Predation on sandpiper nests.—Over the 16 yr of the study, depredation of Spotted Sandpiper nests was due to mice (28%), mustelids (22%), birds (20%), and unknown causes (30%). After mice were removed in 1978, mustelids and birds were the only significant nest predators. There was no indication of tern or gull predation of sandpiper nests. From 1975–1989 avian predators were probably grackles. We had no evidence that turnstones destroyed any nests because they did not spend large amounts of time near the nests. In 1990, however, turnstones were responsible for 2 of 8 sandpiper nests lost due to birds, and were strongly suspected in the other 6 because of frequent presence of turnstones and infrequent presence of foraging grackles near the sites. Spotted Sandpipers do not defend nests from avian predators until eggs hatch, although they might show territorial interspecific aggressiveness (Maxson and Oring 1980, Pickett et al. 1988). After the turnstones left in 1990 there was no destruction of Spotted Sandpiper nests in spite of the presence of a mink family (Fig. 1).

The high incidence of turnstone predation and low incidence of mink predation was contrary to our observations in previous years. We suspected tern colony presence influenced the amount of sandpiper nest predation. Nest-fate data were grouped by the presence of turnstones, mink, and terns (Table 1). To examine the influence of turnstone/tern interactions on sandpiper nest depredation, we compared the fates of early season nests with and without tern presence (Table 1). The presence of terns affected the amount of sandpiper nest depredation ($\chi^2 = 20.42$, $df = 2$, $P < 0.001$). This Chi-square value was partitioned to separate turnstone effects from tern colony effects (Siegel and Castellan 1988). Eighty-five percent of the Chi-square value was due to turnstones, which significantly increased predation on sandpiper nests (partitioned $\chi^2 = 17.33$, $df = 1$, $P < 0.001$), 15% of the Chi-square value was due to a trend toward increasing sandpiper nest depredation in the presence of a tern colony (partitioned $\chi^2 = 3.09$, $df = 1$, $P < 0.1$).

TABLE 1. Fates of Spotted Sandpiper nests, 1975-1990.

	Nest depredated?		Total	χ^2	P
	No	Yes			
No mink, turnstones, or terns	52	6	58		
Early-season				20.42 ^a	<0.001
Turnstones present, no terns	71	43	114	} 3.09 ^b	<0.1
Turnstones & terns present	9	12	21		
Late-season				34.54 ^c	<0.001
Mink present, no terns	12	21	33	} 15.86 ^d	<0.001
Terns & mink present (1990)	10	0	10		
Terns present, no mink (1989) ^e	3	0	3		
Total	157	82	239		

^a df = 2, 2 × 3 contingency table of null and early-season nest fates.

^b df = 1, partitioned early-season χ^2 (Siegel and Castellan 1988); indicates increased turnstone predation in the presence of terns.

^c df = 2, 2 × 3 contingency table of null and late-season nest fates.

^d df = 1, partitioned late-season χ^2 ; indicating reduced mink predation in the presence of terns.

^e Not included in late-season χ^2 analyses.

Because turnstones fed actively on tern eggs at the time sandpiper nests were depredated, we hypothesized that turnstones found sandpiper nests that were near the tern colony while they searched for opportunities to consume tern eggs. All early-season nests destroyed in 1989 and 1990 were destroyed by birds. Of 22 sandpiper nests during this period, those near the tern colony were taken significantly more often (6 of 7) than nests far from the tern colony (6 of 16) (Fisher's exact test, $P = 0.04$).

The lack of mink damage to sandpiper nests in 1990 was surprising because resident mink took large numbers of tern eggs and chicks. When minks were resident in previous years, large numbers of sandpiper nests were destroyed. We hypothesized that the tern colony acted as a decoy, providing a plentiful source of eggs and chicks, which distracted the mink so that they did not search for sandpiper nests. A similar decoy hypothesis for the evolution of lekking behavior was proposed by Phillips (1990). To evaluate this hypothesis, we tested late-season sandpiper nests (when turnstones were not a confounding factor) for effects on hatching success of the presence of mink, nesting terns, or both. Other mustelids were excluded because mink was the only mustelid to cause late-season depredation. Mink presence significantly increased sandpiper nest depredation ($\chi^2 = 34.54$, $df = 2$, $P < 0.001$) and was partitioned to separate effects of mink presence from effects of tern colony presence (Siegel and Castellan 1988). Fifty-four percent of the Chi-square value was due to mink presence signif-

icantly increasing depredation of sandpiper nests (partitioned $\chi^2 = 18.68$, $df = 1$, $P < 0.001$). More importantly, 46% of the Chi-square value was due to colony presence significantly reducing depredation of sandpiper nests (partitioned $\chi^2 = 15.86$, $df = 1$, $P < 0.001$).

DISCUSSION

Early-season depredation.—For clutches initiated before 10 June, most Spotted Sandpiper nest destruction was due to avian egg-predators. We attribute this to several nonmutually exclusive factors. First, early in the season, there was less overall vegetative cover. Spotted Sandpipers most commonly place their nests at the bases of vegetation in semi-open habitat (Oring et al. 1983) and as the season progresses these nests are less visible. Visibility from above can be an important factor in avian predation of some ground nests (Dwernychuk and Boag 1972b), and in this case reduced visibility from the ground (where turnstones and grackles tend to forage) would make finding sandpiper nests more difficult. Second, Ruddy Turnstones were present only during the early-season period. Finally, mink were not present early in the season.

The observed increased depredation of sandpiper nests close to the tern colony could be due to several factors. (1) The conspicuous tern colony might have drawn turnstones into the nest area. Once turnstones foraged on eggs, both tern eggs and nearby sandpiper eggs were consumed. (2) Egg-eating behavior in Ruddy Turn-

stones is probably a learned behavior of recent origin (Brearey and Hildén 1985), perhaps spreading among New World subspecies (Parkes et al. 1971), and could have spread recently to turnstones at LPI. (3) The tern colony might have provided increased opportunities for native turnstones to learn egg-eating behavior. Using plumage characteristics to identify individuals (see Ferns 1978), we observed some turnstones to be especially proficient egg-predators. An increase in the number of turnstones that consumed eggs would also increase the overall amount of predation. (4) Sandpipers near the colony may leave their nests more often due to colony upflights, which exposed the nests to predation. The tern colony alarmed frequently (approximately every 10 min), often for no apparent reason. Nearby sandpipers did not always leave their nests during these disturbances but seemed to leave their nests more often than sandpipers farther from the colony.

Late-season depredation.—Coinciding with the departure of turnstones and growth of concealing vegetation, mink tend to increase their movements and home ranges. Female mink commonly move their young to a new den (Gerrell 1969), and the largest male kits begin to disperse (Gerrell 1970). Because mink find nests by scent or by observing movements of the incubating adult, increases in vegetative cover do not afford increased protection from them. In years without terns present, arriving mink rapidly destroyed most sandpiper nests on LPI, but when the colony was present no nests were taken. Because sandpipers commonly flushed when terns alarmed, we might have expected that tern presence would have made sandpiper nests more conspicuous and susceptible to mink predation, but this was not observed. When terns and mink both were present, mink concentrated on tern eggs and chicks as prey, and ignored sandpipers. Terns were noisy, conspicuous, and plentiful, and we did not observe mink switching to other prey items. Mink prey on adult Red-winged Blackbirds (*Agelaius phoeniceus*) in addition to tern eggs and chicks, so it is unlikely that they had formed a restrictive search image (Tinbergen 1960). Perhaps the ease of locating tern nests and the larger size of tern eggs and chicks made them optimal prey items (Richardson and Verbeek 1986).

Predation and coloniality.—We were unable to address several factors that might influence as-

sociation of a noncolonial species with a colony. The antipredator behavior of the terns did not prevent large-scale depredation of their own nests so direct nest protection was probably not significant for Spotted Sandpipers nesting near the colony. The colony alarm system seemed to be used selectively by the sandpipers and may allow sandpiper adults to avoid predation. Breeding season predation on adults is infrequent (Oring unpubl.), so this is probably of small benefit to the sandpipers.

Early-season sandpiper nests were established before tern colony establishment. Our impression was that late-season nest sites were placed closer to the colony, although we were unable to detect this with our sample size and colony structure. We examined only nest predation because of the difficulty of determining fates of Spotted Sandpiper chicks that did not fledge. Post-hatching predation might be a significant disadvantage to nesting in association with a colony (Dwernychuk and Boag 1972a). Although we do not know fates of chicks that did not fledge, we do know that in 1975, chicks from the single nest that escaped depredation by mink disappeared one day after hatching. In 1990, chicks from 11 of 12 nests from which eggs hatched fledged or were still present on LPI despite mink presence.

Although much has been written about the advantages and disadvantages of coloniality, changes in predation pressure on peripheral species have been studied rarely. Our study of the incidental association of Spotted Sandpipers with Common Terns indicates that there might be advantages and disadvantages to being near a colony, depending on time of year, type of predator, and chance events associated with the presence of ephemeral predators. Similar fine points in predation structure might have influenced the evolution of active single- and mixed-species associations.

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LITERATURE CITED

- BENT, A. C. 1929. Life histories of North American shore birds, part 2. U.S. Nat. Mus. Bull. 146: 288.
- BREAREY, D., & O. HILDÉN. 1985. Nesting and egg predation by turnstones *Arenaria interpres* in larid colonies. *Ornis Scandinavica* 16: 283-292.
- BURGER, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. *Am. Nat.* 123: 327-337.
- , & F. LESSER. 1978. Selection of colony sites and nest sites by Common Terns (*Sterna hirundo*) in Ocean County, New Jersey. *Ibis* 120: 433-449.
- COLWELL, M. A., & L. W. ORING. 1989. Extra-pair mating in the Spotted Sandpiper: a female mate acquisition tactic. *Anim. Behav.* 38: 675-684.
- CROSSIN, R. S., & L. H. HUBER. 1970. Sooty Tern egg predation by Ruddy Turnstones. *Condor* 72: 372-373.
- DWERNYCHUK, L. W., & D. A. BOAG. 1972a. Ducks nesting in association with gulls—an ecological trap? *Can. J. Zool.* 50: 559-563.
- , & ———. 1972b. How vegetative cover protects duck nests from egg-eating birds. *J. Wildl. Manage.* 36: 955-958.
- DYRCZ, A., J. WITKOWSKI, & J. OKULEWICZ. 1981. Nesting of "timid" waders in the vicinity of "bold" ones as an antipredator adaptation. *Ibis* 123: 542-545.
- ERWIN, R. M. 1979. Species interactions in a mixed colony of Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*). *Anim. Behav.* 27: 1054-1062.
- . 1988. Correlates of nest-defense behavior of Common Terns. *J. Field Ornithol.* 59: 135-142.
- EVANS, R. M. 1970. Oldsquaws nesting in association with Arctic Terns at Churchill, Manitoba. *Wilson Bull.* 82: 383-390.
- FERNS, P. N. 1978. Individual differences in head and neck plumage of Ruddy Turnstones (*Arenaria interpres*) during the breeding season. *Auk* 95: 753-755.
- GERELL, R. 1969. Activity patterns of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 20: 451-460.
- . 1970. Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 21: 160-173.
- GÖRANSSON, G., J. KARLSSON, S. G. NILSSON, & S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. *Oikos* 26: 117-129.
- GÖTMARK, F. 1989. Costs and benefits to Eiders nesting in gull colonies: a field experiment. *Ornis Scandinavica* 20: 283-288.
- , & M. AHLUND. 1988. Nest predation and nest site selection among Eiders *Somateria mollissima*: the influence of gulls. *Ibis* 130: 111-123.
- HATCH, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. *Auk* 87: 244-254.
- HILDÉN, O., & S. VUOLANTO. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. *Ornis Fennica* 49: 57-85.
- HÖHN, E. O. 1967. Observations on the breeding biology of Wilson's Phalarope (*Steganopus tricolor*) in central Alberta. *Auk* 84: 220-244.
- KISTCHINSKI, A. A., & V. E. FLINT. 1974. On the biology of the Spectacled Eider. *Wildfowl* 25: 5-15.
- KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. *Ornis Fennica* 34: 1-6.
- KREBS, J. R., & N. B. DAVIES. 1987. An introduction to behavioural ecology, 2nd ed. Oxford, Blackwell Sci. Publ.
- LANK, D. B., L. W. ORING, & S. J. MAXSON. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. *Ecology* 66: 1513-1524.
- LOFTIN, R. W., & S. SUTTON. 1979. Ruddy Turnstones destroy Royal Tern colony. *Wilson Bull.* 91: 133-135.
- MAXSON, S. J. 1977. Common Grackle preys on Spotted Sandpiper chick. *Prairie Nat.* 9: 53-54.
- , & L. W. ORING. 1978. Mice as a source of egg loss among ground-nesting birds. *Auk* 95: 582-584.
- , & ———. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. *Behaviour* 74: 200-263.
- NUECHTERLEIN, G. L. 1981. "Information parasitism" in mixed colonies of Western Grebes and Forster's Terns. *Anim. Behav.* 29: 985-989.
- ORING, L. W., & D. B. LANK. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behav. Ecol. Sociobiol.* 10: 185-191.
- , ———, & S. J. MAXSON. 1983. Population studies of the polyandrous Spotted Sandpiper. *Auk* 100: 272-285.
- , & S. J. MAXSON. 1984. Shorebird migration at Little Pelican Island, Cass County, Minnesota. *Loon* 56: 25-29.
- PARKES, K. C., A. POOLE, & H. LAPHAM. 1971. The Ruddy Turnstone as an egg predator. *Wilson Bull.* 83: 306-308.
- PHILLIPS, J. B. 1990. Lek behavior in birds: Do displaying males reduce nest predation? *Anim. Behav.* 39: 555-565.
- PICKETT, P. E., S. J. MAXSON, & L. W. ORING. 1988. Interspecific interactions of Spotted Sandpipers. *Wilson Bull.* 100: 297-302.
- PIENKOWSKI, M. W. 1984. Breeding biology and population dynamics of Ringed Plovers (*Charadrius hiaticula*) in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. *J. Zool. London* 202: 83-114.

- REED, J. M., L. W. ORING, & J. A. R. ALBERICO. 1991. Common Terns at Minnesota's largest colony: breeding site shift, population decline, and reproductive success. *Loon* 63: 12-16.
- RICHARDSON, H., & N. A. M. VERBEEK. 1986. Diet selection and optimization by Northwestern Crows feeding on Japanese little-neck clams. *Ecology* 67: 1219-1226.
- SIEGEL, S., & N. J. CASTELLAN. 1988. *Nonparametric statistics for the behavioral sciences*, 2nd ed. New York, McGraw-Hill.
- SIEGEL-CAUSEY, D., & S. P. KHARITONOV. 1990. The evolution of coloniality. *Curr. Ornithol.* 7: 285-330.
- TINBERGEN, L. 1960. The natural control of insects in pinewoods, 1. Factors influencing the intensity of predation by songbirds. *Arch. Neerlandaises Zool.* 13: 265-343.
- VERMEER, K. 1968. Ecological aspects of ducks nesting in high densities among larids. *Wilson Bull.* 80: 78-83.
- WALTERS, J. 1957. Gedrag in de legperiode en arbeidsverdeling in de voortplantingstijd bij de Strandpluvier *Charadrius alexandrinus* L. *Ardea* 1: 24-62.
- WITTENBERGER, J. F., & G. L. HUNT. 1985. The adaptive significance of coloniality in birds. *Avian Biol.* 8: 1-78.