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NEST DEFENSE BEHAVIOR OF LESSER GOLDEN-PLOVERS

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ABSTRACT.—The responses of incubating Lesser Golden-Plovers (*Pluvialis dominica dominica*) to a human observer and to avian nest predators were studied at Churchill, Manitoba. Golden-plovers typically left their nest when a human approached to within about 100 m. Usually, birds walked from their nests and vocalized loudly while in full view. As the intruder continued to approach, birds sometimes gave distraction displays, involving "tail down run," "rodent run," and "broken wing" behaviors. Only a few cases of "sitting tight" and "early surreptitious departure" were seen. Some birds flew or ran to a position between the intruder and the nest before performing a distraction display. Both sexes responded similarly toward human intruders. When the observer remained stationary 0.5 m from a nest, about 50% of the males, but none of the females, returned and approached the observer to within a few meters and then performed distraction displays. Reactions toward avian predators were cryptic. With Northern Harriers (*Circus cyaneus*) golden-plovers typically left their nests and stood quietly 100–200 m away; with Herring Gulls (*Larus argentatus*) and Parasitic Jaegers (*Stercorarius parasiticus*) they assumed either an erect, alert position on the nest (predator at a distance) or squatted (predator nearby). Aggressive mobbing of avian predators by golden-plovers was not observed. Low abundance of corvids and humans, and presence of other birds that efficiently drive off avian predators, may account for the golden-plovers' apparent paradoxical combination of conspicuous responses to ground predators and cryptic responses to avian predators. *Received 11 Aug. 1988, accepted 6 March 1989.*

To avoid nest predation, birds may respond to an approaching predator with behavior which is either cryptic (sitting tight, departing stealthily) or conspicuous (e.g., scolding, circling, injury-feigning, attacking). The potentials of the various behaviors differ according to the kind of predator involved. Thus, birds may react differently to predators that are ground-living or flying, visually or scent oriented, and large or small (Sordahl 1981, McCaffery 1982, Gochfeld 1984, Byrkjedal 1987). Conspicuous behavior successfully carried out against one predator species may attract the attention of another which the bird is unable to drive or lure away (McCaffery 1982, Byrkjedal 1987). This may cause constraints on conspicuous antipredator behavior. None of 32 Palearctic shorebirds for which information was available had conspicuous ground predator strategies in the incubation period (scolding, circling, attacking) unless they had aggressive avian predator strategies (10 species, Cramp and Simmons 1983, pers. obs.).

Lesser Golden-Plovers (*Pluvialis d. dominica*) attack avian nest pred-

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ators only in parts of the breeding range, yet their ground predator responses are highly conspicuous (Drury 1961, Parmelee et al. 1967, Sordahl 1981, McCaffery 1982). I studied antipredator behavior of incubating Lesser Golden-Plovers in subarctic Canada in order to identify the species' strategies against ground-living and avian nest predators. The studied population did not attack avian predators, and I discuss whether conflicting cryptic and conspicuous strategies have influenced their antipredator behaviors.

MATERIALS AND METHODS

The study was performed 24 June–20 July 1986 at Churchill, Manitoba, in a 3.75-km^2 area of lichen and sedge tundra (further details, Byrkjedal 1989). The most common potential nest predators were Herring Gulls (*Larus argentatus*) (44% of 36 individual avian predators seen while I watched four golden-plover nests, see below), Parasitic Jaegers (*Stercorarius parasiticus*) (31%), Northern Harriers (*Circus cyaneus*) (17%), and Northern Shrikes (*Lanius excubitor*) (8%). Common Crows (*Corvus brachyrhynchos*) nested on the forest edge; one pair was sometimes seen on the tundra, as were a few Common Ravens (*Corvus corax*). However, no corvids were seen during the nest watches. Red foxes (*Vulpes vulpes*) are the chief mammalian predators at Churchill (Skeel 1983); I saw them 3–4 times in the study area. Arctic foxes (*Alopex lagopus*) and small mustelids may also occur (J. C. Davies pers. comm.).

I found 23 golden-plover nests in the study area. Twenty were found during or just after the egg-laying phase. I individually color-banded seven males and three females. Sexing was easily done in the field by plumage characters, males being more contrast-rich than females (Hayman et al. 1986).

I regarded reactions to humans as comparable to reactions to other ground predators (see Armstrong 1956), and recorded the behavior of golden-plovers to my own intrusions (N = 97) at 22 nests. On these intrusions I walked steadily straight toward the nest while dictating on a tape recorder the reactions of the incubating bird and also of its mate, if present. I also recorded my own and the bird's distance to the nest each time the bird changed behavior. I estimated bird–nest distances visually and recorded my own distances to the nest by pacing. I started the straight approaches 200–300 m from the nests at a point where the sitting bird most likely could see me. These nest visits are referred to as "intrusions." On 63 of the intrusions, I continued to record behavior for 5 min as I sat down 0.5 m from the nest. These observations are analyzed separately.

I found about 12 h incubation stints for each sex, the females sitting at night and the males during the day (unpubl.). Off-duty females were far beyond the territory, while off-duty males were on the territory about 50% of the time. Accordingly, I made intrusions at different times in order to obtain data on both mates and of the males' possible functions as sentinels.

The plovers' reactions to aerial predators were recorded during distant watches (sometimes from a parked car) of four nests (1685 nest min). I also was alert for aggressive predator-mobbing at all times during the field work.

I use Gochfeld's (1984) terminology of antipredator behavior. Definitions of postures are given in Fig. 1. The term "distraction display" refers to behaviors signalling "physical incapabilities" (drawings H through N, Fig. 1).

RESULTS

Reactions to humans.—When I approached golden-plover nests, the sitting bird typically left in an upright walk to one side, often after having

circled the nest at <2 m distance (Fig. 1; data are presented for males only, but data for females were similar). The upright walk often developed into a distraction display, most commonly "tail down run" and "rodent run." As I reached the nest the birds ended their departure and usually stood alert or started circling the nest at about 60 m distance. On 28% (N = 16) of the intrusions (10 nests) the birds, after having departed from the nest, returned and entered a position between the intruder and the nest ("intercepting") before starting a distraction display to one side. In a few cases the birds left their nest surreptitiously. They did so at longer distances (median 175 m) from the intruder than when leaving in full view (males; median 99.5 m, $P < 0.01$, Wilcoxon's Sum of Ranks Test; Fig. 2). Distraction displays started when the birds were at median distances of 17.5 m (males) from the nest and 25 m from the intruder (Fig. 3).

On 17 of 88 intrusions (12 of 22 nests) the birds (males) started to vocalize loudly while they were less than 2 m from the nest, in 6 of these cases (6 nests) even before leaving the nest. Usually the birds started to vocalize 5–10 m from the nest. Golden-plovers always vocalized in "upright walk" and when "standing alert" or "circling at a distance," but they were silent when performing distraction displays and when departing surreptitiously.

To clarify the essential features I classify the responses to humans (from Fig. 1) in four main categories: (1) leaving the nest stealthily with no distraction display, and finally hiding; (2) leaving the nest in full view (walking or flying), no distraction display, finally hiding; (3) leaving the nest in full view, no distraction display, remaining in full view; and (4) leaving the nest in full view, giving distraction display, remaining in full view. The highly conspicuous behaviors (3) and (4) were by far the most common (Fig. 4; the graph includes some intrusions that were not included in Fig. 1 due to loss of details). The birds responded with early surreptitious departure (category 1) in only 10% of the intrusions.

Males and females did not differ in the frequencies of behavioral categories (1)–(4) (χ^2-tests, Fig. 4) or in reaction distances (Wilcoxon's Sum of Ranks Tests; Fig. 2). Off-duty birds contributed little to nest defense. On only six of 19 intrusions did off-duty males warn their incubating mate of my approach, and on one of three intrusions did off-duty females warn. Off-duty birds of either sex stood vocalizing 50–60 m from the nest but never engaged in distraction displays.

On 63 intrusions (20 nests), I remained near the nest (0.5 m distance) for 5 min. Males incubated on 50 of these occasions (20 nests) and females on 13 (11 nests). On 27 of these intrusions (11 nests), the attendant males approached me and then departed in distraction display. None of the females did so (significant difference between mates; Fisher's Test, $P =$

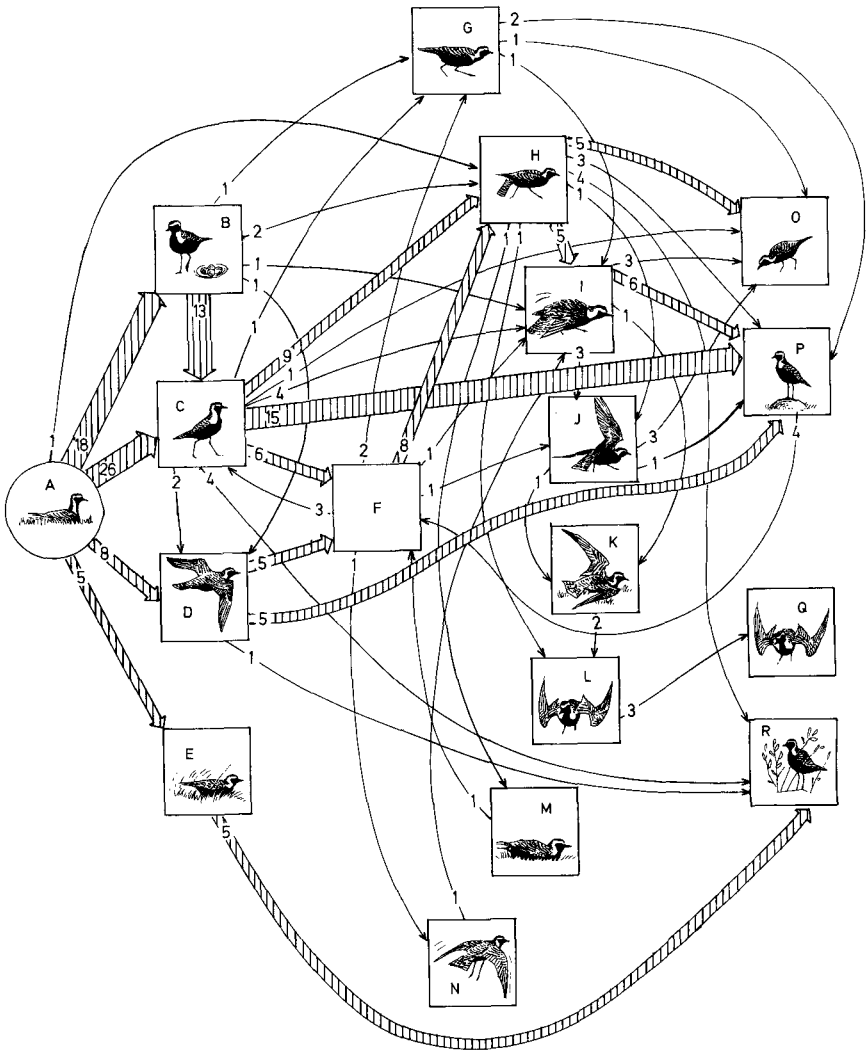

FIG. 1. Reactions of incubating male Lesser Golden-Plovers to a human approaching nests (58 intrusions, 22 nests). O–R are the behaviors seen when the intruder reached nest site. Figures on arrows give the number of approaches on which a behavior was recorded, and thicker arrows represent higher frequencies of occurrence.

A = Incubating male sees intruder
B = Close circling of nest (<2 m distance)
C = Upright run or walk, in full view
D = Flight
E = Surreptitious departure (bird sneaking between tussocks)

0.004, two-tailed). Such behavior (". . . returning toward a recalcitrant intruder as if to recapture its attention") was termed "re-entrapment" by Gochfeld (1984). Re-entrapments were repeated up to 11 times during a 5-min period. The birds started re-entrapment displays at a median distance of 3 m from the intruder and ended their display at a median distance of 6 m, whereupon they started to scold and circle, or returned for another re-entrapment. Several types of distraction displays were usually performed during each re-entrapment (Table 1). Elaborate displays ("broken wing" and "stationary wing-spread" displays) were more common during re-entrapments than during a bird's initial display bout.

Response distances, and the frequencies of behavioral categories (1)–(4) and re-entrapments, did not change significantly over the season (Wilcoxon's Sum of Ranks Tests both on date and on time since egg laying).

Reactions to avian predators. —Distant watches at four nests (1685 min) showed that the responses of incubating birds varied with the species of predator (Fig. 5). The observations concern golden-plover males only, as they incubated during the day, when avian predators were active. The most numerous potential nest predators were Herring Gulls, but incubating plovers showed only slight reactions to them—at most, alertness (<150 m distance) and "semi-squatting" (<70 m distance; the bird sank deeply into the nest but did not stretch the neck along the ground). Four golden-plover nests were situated 85–150 m from Herring Gulls' nests. The birds reacted far more to Parasitic Jaegers, usually by squatting entirely flat on the nest when jaegers came within about 150 m. The plovers

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F = Bird enters position between intruder and nest
G = Crouched run, in full view
H = Tail down run (tail canting, head lowered, bird in full view)
I = Rodent run (tail canting and half spread, wings drooping and quivering, back feathers more or less ruffled)
J = Mobile broken wing display (bird moves along ground with one or both wings flapping)
K = Stationary broken wing display (similar to J but display performed on the same spot)
L = Stationary wing-spread display, bird facing intruder
M = False brooding (bird sits on the ground as if incubating)
N = Impeded flight
O = Distant circling (with false feeding; about 60 m from nest)
P = Standing alert
Q = Continued display when intruder reached nest site
R = Standing concealed behind tussock or bush

Three different types of J and K were seen.

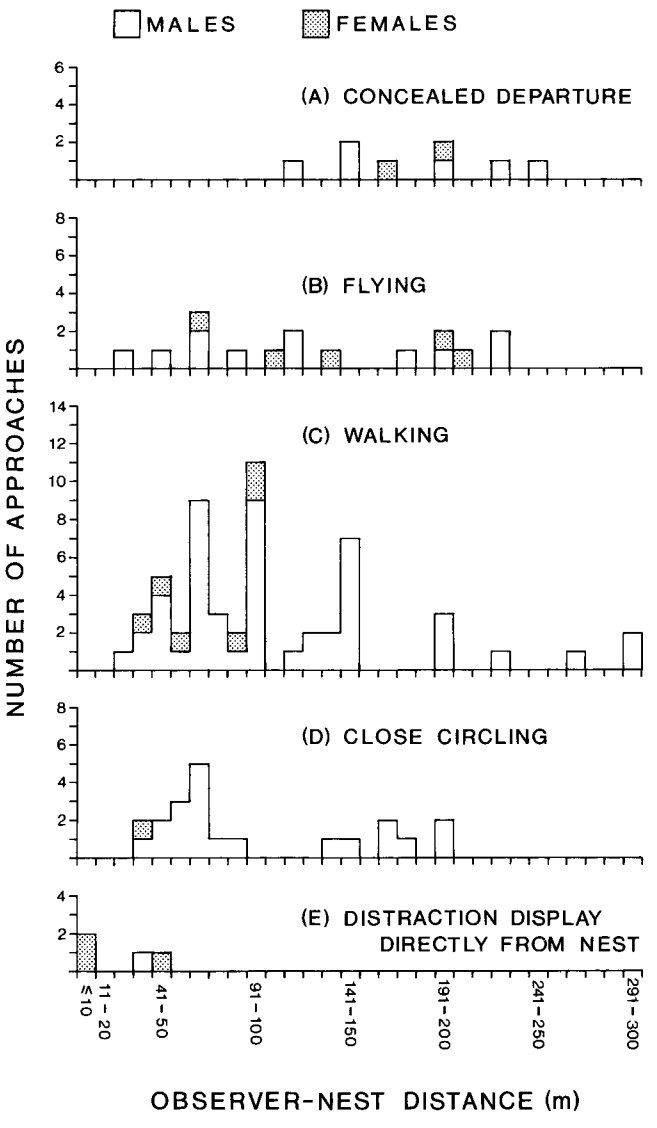

FIG. 2. Distance from approaching observer at which the incubating bird left the nest. (A)–(E) = manner of leaving nest.

also squatted in the presence of a Northern Shrike perched in tree-tops 50–70 m from their nests. Incubating birds left the nest when Northern Harriers were 50–100 m away, flew 100–200 m and stood silently until the harrier was out of sight.

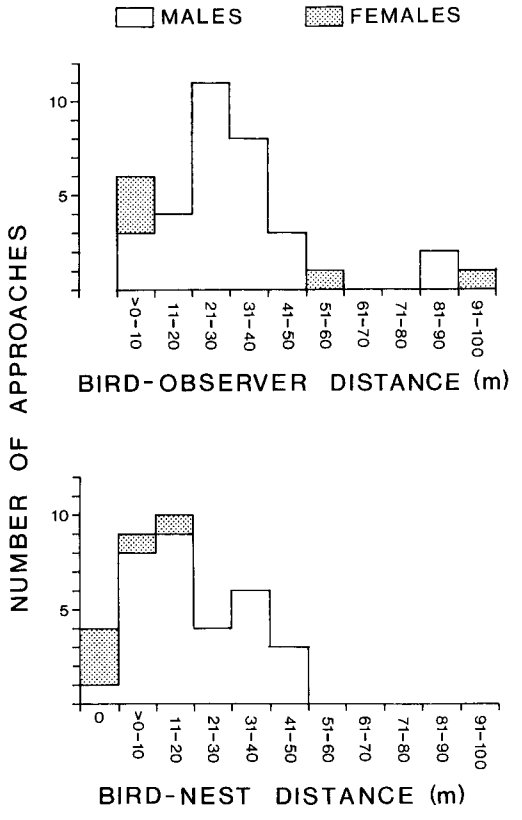

FIG. 3. Bird-to-observer and bird-to-nest distances at which distraction displays started.

The plovers never were seen mobbing any avian predators during 185 hours of field work in the area. However, breeding Whimbrels (*Numenius phaeopus*) were abundant in the area and mobbed frequently. While I watched the four golden-plover nests, jaegers intruding in the golden-plover territories were successfully driven away by Whimbrels on six of 11 observed intrusions and harriers on two of five intrusions.

DISCUSSION

When approached by a ground predator, many shorebirds either leave the nest early and surreptitiously or they sit tight and do not perform any distraction display until flushed almost from underfoot. By "intermediate" responses a bird would "lose the benefits of both behavioral extremes" (Gochfeld 1984). Lesser Golden-Plovers show "intermediate"

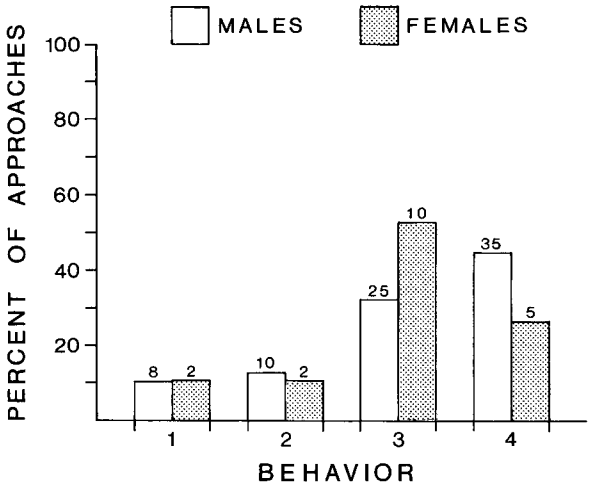

FIG. 4. Frequencies of behavior categories 1–4 on observer's approaches to nests (numbers above bars indicate number of approaches).

1 = Surreptitious departure, bird staying hidden
2 = Departure fully visible (flight or run), no distraction display, bird finally hiding
3 = Departure fully visible, no distraction display, bird remaining fully visible
4 = Departure fully visible, distraction display given, bird remaining fully visible.

behavior, as they leave early and highly conspicously. In the case of human intruders, they depart from the nest at about 100 m distance, usually with loud vocalizations and no attempts to conceal themselves. The effect of this behavior is probably to disturb the search of an approaching predator long before it has come within "detectability distance" of the nest. The birds resort to "injury feigning" behavior only if the intruder continues to approach the nest. Usually such behavior was elicited when the intruder was considerably less than 50 m from the nest.

The ground predator responses of Lesser Golden-Plovers are completely different from those of Greater and Pacific (Lesser) golden-plovers (*Pluvialis apricaria, P.* [*dominica*] *fulva* [probably a separate species (Connors 1983)]) and Black-bellied Plovers (*P. squatarola*), all of which practice an early surreptitious departure. The latter two often reappear after the departure and distract or chase the ground predator (Drury 1961, Sauer 1962, Flint and Kondratjew 1977), while the former remains cryptic. In addition, Greater, and sometimes Pacific (Lesser), golden-plovers sit tight as an alternative to early departure (Williamson 1948, Sauer 1962, Ratcliffe 1976, Byrkjedal 1987).

Early conspicuous departure was not a specific reaction to humans, as

TABLE 1
DISTRACTION DISPLAYS GIVEN BY LESSER GOLDEN-PLOVER MALES DURING 71 RE-ENTRAPMENTS[a]

Behavior[b]	Number of displays observed
Tail down run (H)	39
Rodent run (I)	30
Mobile broken wing display (J)	50
Stationary broken wing display (K)	60
Stationary tail down/wing-quiver[c]	6
Stationary wing-spread display, facing intruder (L)	43
False brooding (M)	1
Total	229

[a] Displays given at close range while observer sat 0.5 m from nest (N = 20 nests).
[b] The letters in parentheses refer to description of the postures given in Fig. 1.
[c] Posture similar to "tail down run," but bird stationary with wings quivering.

a bird dog elicited the same behavior (tested at four nests; see also Armstrong 1956). In fact, early conspicuous departure would be a poor adaptation to human predation, as humans could easily use such behavior to locate nests. Lesser Golden-Plover nests are probably among the easiest shorebird nests to find, while nests of Pacific (Lesser) Golden-Plovers, Black-bellied Plovers, and in particular Greater Golden-Plovers, can only be found with considerable effort (Williamson 1948, Ratcliffe 1976, Portenko 1981, Byrkjedal 1987). The Lesser Golden-Plover may be less well adapted to human nest predation than the other *Pluvialis* plovers due to a virtual lack of humans over much of its breeding range (Lee and DeVore 1968, Godfrey 1979, Hayman et al. 1986).

The Lesser Golden-Plovers at Churchill showed markedly cryptic responses to flying predators in spite of their conspicuous ground predator reactions. Being visually oriented, avian predators could be attracted to a nest site by conspicuous responses to ground predators by the attending bird. In the other *Pluvialis* plovers, reactions during the incubation period to both ground-living and flying predators are either strongly cryptic (Greater Golden-Plovers: Byrkjedal 1987) or conspicuous (Black-bellied Plovers: Drury 1961, Flint and Kondratjew 1977; Pacific (Lesser) Golden-Plovers: Sauer 1962). Aggressive mobbing of flying predators has been reported from some Lesser Golden-Plover populations (Drury 1961, Sordahl 1981, McCaffery 1982) but was not seen at Churchill. The apparent paradoxical combination of cryptic and conspicuous strategies of these golden-plovers might result from: (1) differences in diurnal activities of avian and ground-living predators, (2) low abundance of avian predators,

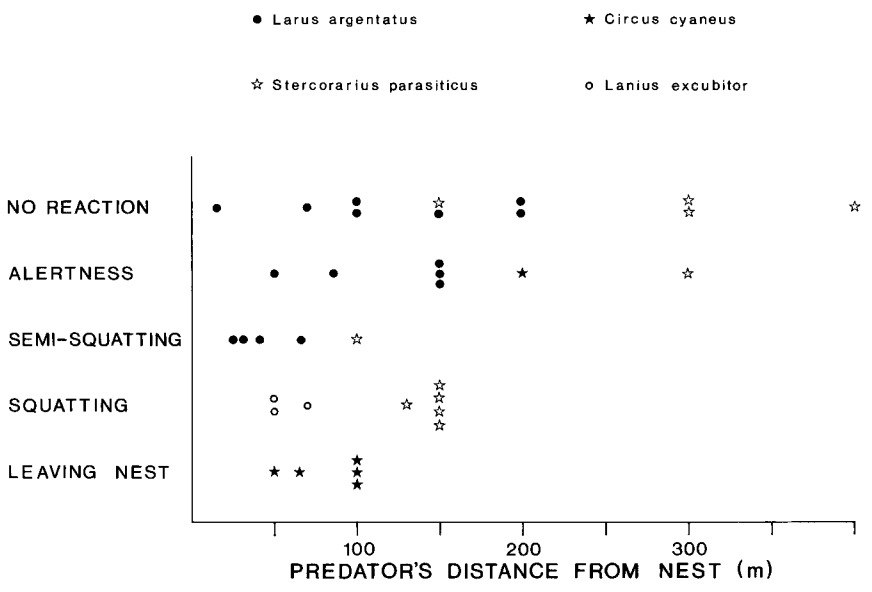

FIG. 5. Reactions of incubating golden-plover males to avian predators. The predators flew about 1–15 m above the ground, except Northern Shrikes, which perched 2–3 m above the ground in tree-tops most of the time. Data from four nests. Each symbol represents one overflight.

and (3) plovers breeding near other aggressive species (cf. Göransson et al. 1975, Dyrcz et al. 1981).

Many ground predators (e.g., red, but not Arctic, foxes) tend to be crepuscular while avian predators operate during the day. This difference in diurnal rhythm may ease the conflict between cryptic and conspicuous behaviors, but probably less so in high latitudes where nights are shorter and lighter than at low latitudes. At Churchill, I repeatedly saw foxes active in the middle of the day. Avian predators were abundant at Churchill. On average golden-plover territories were overflown about once per 45 min. Nevertheless, the chances that avian predators should detect conspicuous ground predator responses might have been slight. The species that were most abundant (Herring Gulls, Parasitic Jaegers, Northern Harriers) usually search in swift flight. Their presence over a golden-plover territory is therefore very short, and the chances are small that it should coincide with an intruding ground predator. Although Common Crows and Common Ravens were observed, they were relatively scarce on the Churchill tundra. Corvids are extremely potent nest predators, likely to capitalize on conspicuous ground predator behaviors due to their persis-

tent search (fairly slow flight, frequent use of vantage points, watching from concealment; pers. obs.), and high mental abilities (e.g., Simons 1976, Montevecchi 1978, Sonerud and Fjeld 1987). Corvids are severe nest predators on the breeding grounds of Greater Golden-Plovers (Ratcliffe 1976; Parr 1980; Langslow 1983; Byrkjedal 1980, 1987) and may have put constraints on conpicuous antipredator behavior in this species. The tundra-nesting *P. squatarola, P. fulva,* and *P. d. dominica* may have experienced less constraints from corvids. Corvids need trees or cliff-ledges for nesting and are therefore less abundant on the flat and bare tundra (Dement'ev and Gladkov 1954, Godfrey 1979).

Aggressive predator-mobbers at Churchill were Whimbrels, Hudsonian Godwits (*Limosa haemastica*), and Bonaparte's Gulls (*Larus philadelphia*) (Hagar 1966, Jehl and Smith 1970, Skeel 1983, pers. obs.). Most golden-plover territories overlapped with Whimbrel territories. Whimbrels efficiently chased away flying predators, attacking from a distance of 100–200 m. This could have decreased the possibilities for flying predators to take advantage of the golden-plovers' conspicuous ground predator responses and also have reduced the need for golden-plovers to aggressively mob avian predators.

Summing up, the study shows that incubating Lesser Golden-Plovers use conspicuous ground predator responses in spite of relying on cryptic behavior against flying predators. Low nest predation pressure from corvids and humans, as well as the presence of other birds that efficiently chase avian predators, are likely factors accounting for this.

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