ANTIPREDATOR BEHAVIOR AND BREEDING SUCCESS IN GREATER GOLDEN-PLOVER AND EURASIAN DOTTEREL[1]

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Abstract. Breeding success and antipredator behavior of Greater Golden-Plovers (*Pluvialis apricaria*) and Eurasian Dotterels (*Charadrius morinellus*) were studied in Norway over seven summers in an area 1,200 to 1,350 m altitude. Behavior was recorded in a standardized manner on nest inspections, on approaching parent birds with chicks, and by observing reactions to overflying predators on scheduled observation bouts. Red foxes (*Vulpes vulpes*), Common Ravens (*Corvus corax*), and Mew Gulls (*Larus canus*) were the most important nest and chick predators in the area. Nest predation was calculated from exposure time. During incubation both species either sneaked away from the nest when approached by a human (golden-plovers at a much larger distance than dotterels) or sat tightly and flushed at a short distance giving distraction display. "Sneaking" had a positive effect on nest survival, and ground distraction displays had a better effect on nest survival than flight distraction displays. After hatching, golden-plover parents exposed themselves to an approaching human at several hundred meters distance by loud alarm calls and by encountering the intruder, whereas dotterels kept unobtrusive until approached to about 40 m, and upon further approach finally gave distraction displays on the ground. Avian predators at a longer distance (>300 m) from nest or chicks at most aroused alertness, while at close quarters (<50 m) they induced golden-plovers to squat flat, while dotterels exposed themselves by "tail-flagging." Nest loss was greater for golden-plovers (78%) than for dotterels (47%), while chick loss was greater for dotterels (65%) than for golden-plovers (28%). The difference in nesting success and antipredator behaviors is discussed in terms of greater detectability in golden-plovers than dotterels, and of biparental (golden-plover) versus uniparental (dotterel) care.

Key words: Distraction displays; detectability; nest and chick losses; plovers; Norway.

INTRODUCTION

The nests and chicks of ground-nesting birds are particularly vulnerable to predation (Armstrong 1954, Lack 1968). Through selection, such birds have evolved adaptations favoring concealment and/or certain behavioral responses to the predator. The nature of the latter (whether a bird hunting visually or a mammal hunting by scent) often elicits very different antipredator strategies. Many shorebirds nesting in vegetative cover, e.g., snipes, sit tightly, while e.g., plovers nesting on open ground often leave their nest early in the presence of a predator (Gochfeld 1984), implying that decision rules for response distances and types of reactions strongly depend on detectability.

In biparental breeding systems, certain antipredator adaptions (like standing guard or driving off predators by mobbing) are enhanced through the cooperative efforts of both parents, with the resultant behaviors often boldly conspicuous. By contrast, uniparental systems should involve selection of less bold and more cryptic behavior.

I studied antipredator behaviors and the impacts of predation on the nests and chicks of biparental Greater Golden-Plovers (*Pluvialis apricaria*) and uniparental Eurasian Dotterels (*Charadrius morinellus*) breeding sympatrically on a mountain plateau in southern Norway. As both species were studied contemporaneously and in the same area, they were exposed to the same predation pressure. I primarily discuss to which degree their antipredator responses are influenced (1) by detectability, and (2) by their biparental and uniparental breeding systems.

STUDY AREA AND METHODS

The study site was on Hardangervidda, Norway (60°23′N, 07°38′E) in the middle alpine zone at about 1,200 to 1,350 m above sea level. Work was conducted during the summers of 1977 to 1981, 1984, and 1985. For additional details concerning the site, see Kålås and Byrkjedal
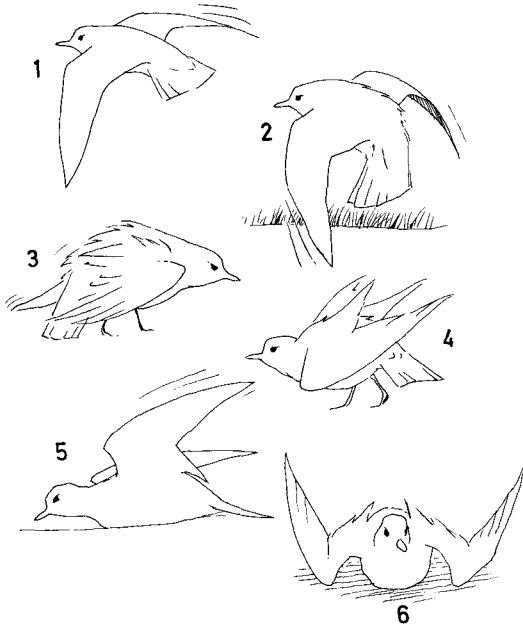
FIGURE 1.   Classification of distraction displays given by birds flushed from the nest. 1, weakly impeded flight; 2, strongly impeded flight; 3, rodent run; 4, mobile injury feigning; 5, stationary injury feigning; 6, aggressive distraction display. Motor patterns of 1, 2, and 3 were highly stereotypic, while 4 and 5 showed some variation (cf. illustrations in Simmons 1955).

(1984). The most important predators in the area were the Common Raven (*Corvus corax*), Mew Gull (*Larus canus*), and Red Fox (*Vulpes vulpes*) (Byrkjedal 1980).

Portions of the study area were searched systematically (almost every day, and usually by two persons) for nests or chicks. Usually nests were found by flushing the incubating bird, or by observing a bird returning to its nest. In 1981, a trained pointing dog was used to locate some of the nests.

I inspected nests at intervals to follow nesting success. Nests showing clear signs of predation (eggshells, etc.) and nests that became empty at times when hatching was not expected were counted as robbed. I excluded a few nests for which it was uncertain whether the eggs had hatched or been robbed. Since only a few nests were monitored from egg laying, I calculated nesting success from exposure time (Mayfield 1975). As there is a marked diurnal rhythm in the feeding time of the predators (birds are active during the day and foxes at night) I considered it justifiable to regard "nest days" as discrete
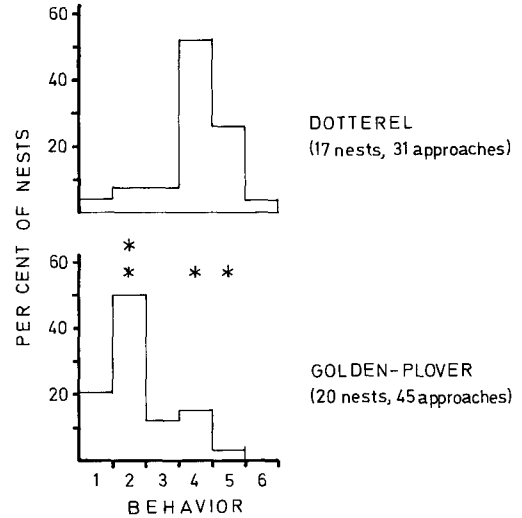

FIGURE 2.   Frequencies of distraction displays (see Fig. 1) given in response to the observer. Asterisks indicate significant differences (*P < 0.01, **P < 0.001) between the species (χ^2-tests).

events and to use Mayfield's (1975) original method for testing differences between nest survival rates.

After leaving the nest golden-plover chicks were far more difficult to relocate than dotterel chicks. Thus, data on complete brood size in golden-plovers were only obtained around fledging, while several unfledged dotterel broods were inspected more than once.

When flushing birds from nests or encountering parents with broods, I considered myself as a simulation of a ground predator, and recorded all antipredator behavior (flushing distances and types of reactions). Distraction displays (Fig. 1) were recorded over defined sequences: either up to the moment the bird disappeared or stood quietly at 100 to 200 m distance, or, (for some dotterels) until the first "reentrapment" occurred (term used by Gochfeld [1984] for cases where a displaying bird returns and starts distracting once more if not followed by the predator on the first distraction attempt). In 1985 I placed a stuffed fox 10 m from five golden-plover nests, three dotterel nests and near five golden-plover broods, and studied the behavior of the birds from a long distance for 15 min. The birds reacted in the same way as they did in the presence of a human. Behavioral responses to avian predators overhead were recorded during observation bouts, both for birds on nests and with broods.

TABLE 1. Responses to human approaching nest.

	Flushing distance (m)						
	0–5	6–10	11–15	16–20	21–50	51–100	>100
Golden-plover (46 nests, 111 approaches)							
Distraction display given	39	23	4	2	2	—	4
Sneaking away, no distraction	—	—	—	—	—	—	37
Dotterel (37 nests, 90 approaches)							
Distraction display given	41	—	—	—	—	—	—
Sneaking away, no distraction	—	5	4	9	18	5	8

Since I could not obtain all types of information from all nests, sample sizes vary in different calculations.

RESULTS

RESPONSES TO GROUND PREDATORS (MAN)

Golden-plovers sneaked away from their nests significantly more often than dotterels when approached by an observer further than 100 m from the nest ($\chi^2 = 58.657$, $P < 0.001$), while dotterels let the observer approach closer than 5 m before flushing significantly more often than golden-plovers ($\chi^2 = 27.876$, $P < 0.001$, Table 1). All dotterels that flushed from the nest at short distances (0 to 5 m) performed distraction displays, while none of those leaving the nest at longer distances did so (Table 1). All golden-plovers performed distraction displays when flushed from the nest from up to 50 m distance, and some did even when the observer was still ≥100 m away. "Strongly Impeded Flight" was recorded at sig-

nificantly more of the golden-plover nests than dotterel nests, while significantly more of the dotterels performed "Mobile Injury Feigning" and "Stationary Injury Feigning" than did golden-plovers (Fig. 2).

When approached by a human, sneaking away from the nest was seen at least once in 37% of 46 golden-plover nests and 54% of 37 dotterel nests. Such nests survived significantly better in both species, compared to nests where sneaking never was observed (Table 2). Nest survival and distraction intensity were positively related in both species, as nests where ground displays were given survived better than nests at which only flight displays were recorded. However, for dotterels but not for golden-plovers, survival was significantly better in nests where stationary displays were given than in nests with only mobile displays (Table 2).

After the eggs had hatched, adult golden-plovers were very conspicuous. They started to give loud alarm calls on generally more than 200 m

TABLE 2. Nest survival in relation to manner of leaving nest when approached by human.

	Estimated nest survival (%)	χ^2	P	n
Golden-plover				
Sneaking away[1]	29.9	5.923	<0.02	27
Sitting[1]	20.7			
Flight distraction[2]	26.6	5.026	<0.005	20
Ground distraction[2]	53.6			
Mobile distraction[2]	32.5	1.509	n.s.	20
Stationary distraction[2]	54.1			
Dotterel				
Sneaking away[1]	79.3	8.234	<0.001	26
Sitting[1]	51.1			
Flight distraction[2]	2.4	121.49	<0.001	17
Ground distraction[2]	88.3			
Mobile distraction[2]	58.2	3.918	<0.05	17
Stationary distraction[2]	81.6			

[1] "Sneaking" includes all nests where this behavior was observed at least once; in the category "sitting" sneaking was never observed and the birds always gave distraction displays when flushed from nest.
[2] Including all the "sitters" and some of the "sneakers." Flight distraction = 1 and 2, Fig. 2; ground distraction = 3–6; mobile distraction = 1–4, stationary distraction = 5–6.

TABLE 3. Responses to approaching human after hatching.

	Golden-plover			
	Single males $(n = 6)$	Males in pairs $(n = 19)$	Females in pairs $(n = 21)$	Dotterel males $(n = 11)$
First response				
Loud alarm call	6	19	21	—
Approaching[1]	—	—	—	1
Retreating[2]	—	—	—	6
Distraction display	—	—	—	4
Reaction distance, meters ($\bar{x}$, ±SD)	288 ± 128	343 ± 162	236 ± 138	40 ± 32
Final response				
Taking flight	6	18	20	—
Distraction display	—	1	1	11
Reaction distance, meters ($\bar{x}$, ±SD)[3]	41 ± 9	38 ± 11	54 ± 4	16 ± 9
Sitting alert on stone or tussock when approached	2	19	13	2

[1] Golden-plover: After giving alarm call, 8 of the paired males, 1 of the single males, and 5 of the females approached the observer.
[2] Golden-plover: After giving alarm call, 1 of the paired males, 4 of the single males, and 8 of the females retreated from the approaching observer.
[3] Golden-plover: Distance for taking flight; distraction display was released at 4 m (both mates simultaneously).

distance, often encountered the observer, stood well exposed on top of stones or tussocks, and finally retreated by taking flight when on average 38 to 45 m from the observer (Table 3). In contrast, dotterels remained silent (to the observer's ear) and did not react until the observer was on average 40 m away, by retreating, approaching, or performing distraction displays. When standing, they were partly hidden by stones or tussocks. All dotterels ended up in distraction display at close range (types 3 to 7, Fig. 1), while for golden-plovers this occurred once (both members of a pair) in 25 approaches.

Golden-plover males and females showed slightly different reactions (Table 3). Females started calling at shorter distances than their mates ($t = 2.100$, $P < 0.025$), took flight at longer distances ($t = 1.985$, $P < 0.005$), and more often ran away upon the observer's appearance ($\chi^2 = 7.134$, $P < 0.001$). In 17 of 18 cases the male was the first to give an alarm call, the female in only one case (Fisher's Test, $P \ll 0.0001$). Females sat exposed on stones and tussocks less often than their mates (Fisher's Test, $P = 0.0050$). The average reaction distance of six single golden-plover males with chicks was intermediate between those of males and females in pairs.

RESPONSES TO AVIAN PREDATORS

Both golden-plovers and dotterels showed only alertness or no response at all to a flying predator (Common Raven, Mew Gull) at a distance of

some hundred meters from nest or chicks (Table 4). When aerial predators passed nests or chicks less than 50 m away, golden-plovers squatted flat (in the case of ravens) or showed alertness (in the case of gulls), whereas dotterels performed "tail-flagging" (Fig. 3) a distance from the nest or chicks (for both ravens and gulls). In this display, the attending bird quickly ran 10 to 15 m from the nest or chicks and then stopped abruptly with breast on the ground and the white undertail coverts exposed. I was able to study the predator's reaction to tail-flagging only twice; in both cases the predator (gull) took no notice, and in neither of the observed cases of tail-flagging did the predator alight or start a search.

In one observed case of nest predation by a raven, a golden-plover crouched on the nest until almost hit by the swooping raven. When squatting flat by overflying ravens in the posthatching period golden-plovers were not covering the chicks, which were dispersed nearby, crouching motionless.

BREEDING SUCCESS

The estimated total nest predation was 47.4% for dotterels over the average 25-day incubation period (16 of 53 nests robbed over 630.5 nest days), and 78.2% in golden-plovers (27-day incubation period, 27 of 51 nests robbed over 492 nest days). The difference is statistically significant ($\chi^2 = 44.595$, $P < 0.001$).
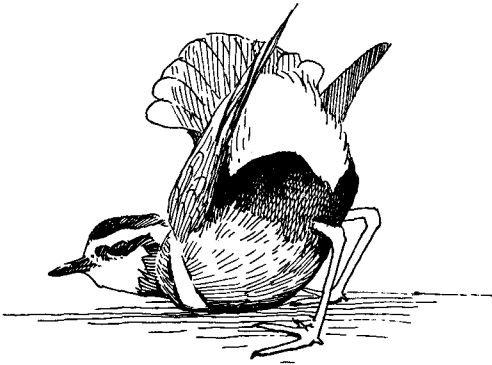
Golden-plovers sitting on the nest were more

FIGURE 3.   Tail-flagging by dotterel when the nest is overflown by an aerial predator.

easily found by scent than dotterels, as the pointing dog used in 1981 found significantly more of the former (7 of 12 available golden-plover nests vs. 1 of 10 dotterel nests, Fisher's Test, $P = 0.038$). (The dog responded and pointed only to nests with a bird.)

Predators usually took whole clutches. The daily disappearance rates of single eggs were only 0.05% in the dotterel (1 of 159 eggs, 1,861.5 egg days), and 0.46% in golden-plovers (8 of 187 eggs, 1,859 egg days). These rates are not statistically different ($\chi^2 = 0.3935$).

In golden-plovers 2 of 67 eggs (17 nests) were infertile, as were 2 of 77 dotterel eggs (26 nests), implying a hatchability of 97.0% and 97.4%, respectively. Relocation of 16 dotterel broods in their first and second week gave a daily disappearance rate of 12% according to the Mayfield (1975) method (21 chicks disappeared during 175.7 chick days), clearly too high a figure for the whole season as chick loss is likely to be highest soon after hatching (Nethersole-Thompson 1973). Taking into account mean clutch sizes,

TABLE 5.   Estimated minimum brood loss from observed clutch sizes around fledging.

	Number of chicks	Observed broods	Numbers of chicks estimated hatched from these broods[1]	% Chicks lost
Golden-plover	19	8	26.2	27.5
Dotterel	9	7	25.8	65.1

[1] Taking into account predation rate on single eggs and hatchability.

predation on single eggs, and hatchability, a minimum chick loss of 27.5% for golden-plovers and 65.1% for dotterels can be estimated (Table 5) from brood sizes at the age of fledging (30 days for golden-plovers, 26 days for dotterels, pers. observ.). The amount of chick loss caused by predation is unknown, but chicks of both species were found in Mew Gull pellets in the area (Byrkjedal et al. 1986).

Mean clutch sizes were 3.87 for the golden-plover (55 c/4, 8 c/3), and 2.98 for the dotterel (50 c/3, 1 c/2). From mean clutch sizes, hatchabilities and losses, 100 nests are estimated to produce about 50 fledged chicks in both species (Table 6).

DISCUSSION

The behaviors recorded during the incubation period concern males. Dotterel males usually incubate alone (Kålås and Byrkjedal 1984) and golden-plover males sit on the nest during daytime for about 12 hr while their off-duty females are far away from the territory (Byrkjedal 1985). Thus, both species incubate in the absence of a warning mate, and should therefore be expected to have similar antipredator responses in the incubation period, assuming a similar detectability

TABLE 4.   Responses to overflying Mew Gulls and Common Ravens.

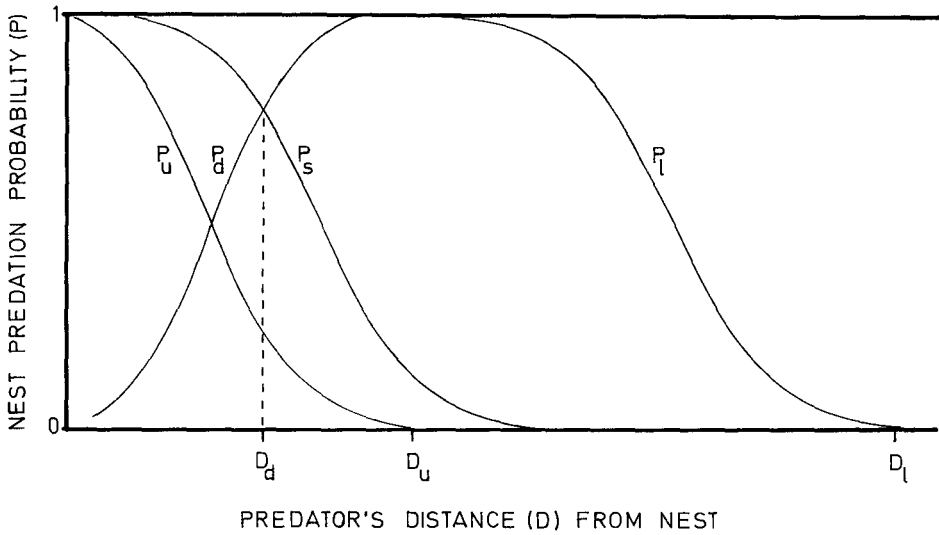|	Predator 300 to 1,000 m away		Predator <50 m away			Observ. time (min)	No. nests or broods
	No response	Alertness	Alertness	Squatting flat	Tail-flagging		
Incubation							
Golden-plover	4	1	—	5[1]	—	553	2
Dotterel	1	3	—	—	8	526	4
Posthatching							
Golden-plover	—	7	3[2]	3[1]	—	4,654	5
Dotterel	—	1	—	—	1	152	5

[1] Common Ravens.
[2] Mew Gulls.

FIGURE 4. Suggested relationship between nest predation probability and the predator's distance from the nest, based on detectability curves for: a bird in the act of leaving the nest without giving distraction display (P_1), a bird sitting on the nest (P_s), an unattended nest (P_u), and the reciprocal probability (P_d) for deflecting a predator by display when a bird is flushed from the nest. Further explanation: see Discussion.

for the two species. In the presence of a ground predator both species either leave the nest early, or they sit tightly and display when flushed from a short distance, but the reaction distances and display intensities are different. They also differ in their reactions to avian predators.

Detectability is presumably a monotonically decreasing function of the distance from the predator to the nest, as suggested in Figure 4 (see Burnham et al. 1980 for likely shape of detectability curves). The decision to leave the nest early or sit tightly should depend on the differences between detectability (and hence, the probability (P) for nest predation) of a bird in the act of leaving the nest (P_1), of a bird sitting on the nest (P_s), and of an unattended nest (P_u), and also on the probability (P_c) that a predator will chase

TABLE 6. Estimated reproductive success in 100 golden-plover and dotterel nests.

	Golden-plover	Dotterel
Number of eggs laid	387	298
Number of eggs after nest predation	84.4	156.7
Number of eggs after partial predation	75.1	154.6
Number of eggs hatching	72.8	150.5
Number of fledglings	52.9	52.5

a displaying bird, which should be negatively related to the distance to the bird. The probability (P_d) for nest predation during distraction display is $(1 - P_c)$.

Provided $P_u < P_s$, early departure from the nest should pay before the predator has approached the distance D_1 from the nest. If the predator is discovered at $<D_1$, the bird should remain tightly on the nest and not start performing distraction displays until the predator approaches D_d. This explains the "bipolarity" in the nest departure distance, commonly observed in birds (Gochfeld 1984), and recorded in the present study. As the gundog did not find unattended nests, the scent stimulus from the nest is apparently chiefly from the sitting bird itself.

As early departure was found to be a more efficient response than merely sitting tightly, there should be a strong selection for early departure. However, egg chilling and a possible high P_1 to avian predators should select for sitting. D_1 should, therefore, be the optimal point for early departure.

Low detectability expectedly skews the curves in Figure 4 to the left. This is supported by the present study, as the dotterel (lower detectability to the gundog and lower recorded nest predation than for golden-plover) had the shortest ground-predator reaction distances of the two species,

both in early departure and when sitting tightly. For early departure to be a good option, the incubating bird must discover the predator at a sufficiently long distance, presumably enhanced by a flat topography. Ratcliffe (1976) noticed that in Britain there were differences between golden-plover populations in their tendency to leave the nest early.

When a bird performs distraction display the impression of its physical incapability varies with the types of displays given. The present study indicates that displays along the ground (high degree of incapability) are more efficient than displays performed while flying away from the nest. Provided the birds are able to meet the risk to themselves from high incapability displays by hyperalertness (Gochfeld 1984), the selection for such displays should increase with decreasing flushing distance, especially as the difference between P_u and P_s may decrease. This is supported by the present study, as the dotterel, which has the shortest flushing distance of the two species, also showed the highest frequency of ground displays. Such displays seemed to have greater effect on nest survival for the dotterel than for the golden-plover.

The detectability to visually oriented (avian) predators is obviously different from detectability to predators hunting by scent. In case of aerial predators either P_1 is skewed far to the right relative to that for ground predators, or $P_u \gtrsim P_s$, since early departure is not practiced by the studied species in the presence of avian predators. For dotterels P_s for avian predators may be higher than for golden-plovers, as dotterels leave the nest and tail-flag when a predator flies overhead, while golden-plovers squat flat. A reaction to flying predators similar to the tail-flagging of the dotterel, has been seen in incubating Ringed Plover (Charadrius hiaticula) (Vaughan 1980), which breeds in very open habitat, while squatting flat on the nest is considered the most common response to avian predators by shorebirds that do not attack (Gochfeld 1984). Both species showed the same response to avian predators after hatching as they did before hatching.

Several shorebirds approach a ground predator after early departure and perform distraction, scolding, or mobbing (Gochfeld 1984). In doing so they may display at the optimal display distance (P_d independent of the predator's distance from the nest), when the predator is still beyond the distance D_u. However, as such behavior renders the birds more conspicuous to avian nest predators than merely early surreptitious departure, this strategy should incur a risk if the birds are not able to distract or actively drive away avian predators. Such a strategy has been reported for Black-bellied Plovers (Pluvialis squatarola), which effectively "dive-bombs" avian predators (Parmelee et al. 1967, Flint and Kondratjew 1977, Portenko 1981). Neither of the two species in the present study were seen to drive away aerial nest predators. In the study area a number of Mew Gulls were almost constantly on the wing and ravens were frequent.

However, after hatching, the golden-plover does practice a highly conspicuous 'approach and scold' behavior, while the dotterel still acts cryptically in the presence of humans (displaying only at close range). Such behavior may be less risky after hatching as chicks are dispersed, unlike the eggs, that are confined to a fixed location all the time. The difference between the species' behavior after hatching may reflect the differences between biparental and uniparental care. Cooperation between the mates is apparently important in the active antipredator behaviors of the Black-bellied Plovers (Flint and Kondratjew 1977). Admittedly, single golden-plover males with chicks did not respond fundamentally differently from golden-plover pairs, and Purple Sandpipers (Calidris maritima) breeding in the same area utilize the approach and scold behavior after hatching in spite of having uniparental chick care (pers. observ.). However, both these species enjoy female participation in incubating, which enables extensive feeding during the incubation period. Golden-plover males improve their body condition during incubation, probably enabling them to absorb high energetic costs during chick care (for effect on vigilance, see Byrkjedal 1985), whereas dotterel males lose weight (Kålås and Byrkjedal 1984). Thus, constraints from uniparental incubation cannot be ruled out as a factor favoring cryptic chick-tending behavior. Also the high estimated chick loss for dotterels suggests a cost of being uniparental.

To sum up, evidence suggests that the birds' reaction distances and display patterns in the presence of a predator depend on detectability. Those display types which signal high physical incapability are the most efficient ones. Early surreptitious departure is apparently a more efficient reaction to ground predators than merely sitting tightly, but may involve the cost of increased

detectability to visual predators. Uniparental care may favor cryptic behavior.

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