

FACTORS AFFECTING PARENTAL BEHAVIOR IN SEMIPALMATED PLOVERS

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ABSTRACT.—We studied Semipalmated Plovers (*Charadrius semipalmatus*) during two field seasons in Churchill, Manitoba, to examine the contribution of males and females to parental care during incubation and chick rearing, and to test the hypothesis that birds nesting in habitats with higher visibility and more food (i.e. coastal habitats) tend chicks less closely than birds nesting in habitats with lower visibility and less food (i.e. inland habitats). Males at the coast flew and vocalized more than females during the chick-rearing period, and, in both areas, incubated during the darkest hours (2400 to 0220), whereas females incubated from 0220 to 0530. Incubation shifts were longer at night than during the day but did not differ between sexes or habitats. Incubation by males during the darkest hours may allow females to feed when invertebrates are most active, and may be a mechanism by which females obtain a better energy balance. Coastal habitats contained more food than inland habitats and more potential predators of both chicks and adults. During incubation, parents in coastal habitats exhibited fewer vigilant behaviors than parents in inland habitats, although the overall time budgets for the most common behaviors did not differ between habitats. Parent-chick distances did not differ between coastal and inland habitats, although as chicks became older, they foraged farther from their parents and were brooded less frequently. The apparent response of adults to predators did not differ between the two habitats. The time that parents spent brooding chicks was negatively correlated with ambient temperatures but was not affected by habitat. Received 17 June 1996, accepted 14 July 1997.

SOCIALLY MONOGAMOUS SHOREBIRDS generally show few sex differences in their contribution to parental care, with the exception that during the chick-rearing period females depart earlier for migration in many species (Ashkenazie and Safriel 1979, Gratto-Trevor 1991, Székely and Williams 1995). In the Killdeer (*Charadrius vociferus*), females also feed more during the late incubation stage than do males, possibly to procure reserves for subsequent nesting attempts (Brunton 1988a). An apparent division of labor occurs in the pattern of nocturnal incubation of plovers (*Charadrius* spp.), with males incubating more often during the darkest hours than females (Warnock and Oring 1996). Beyond these relatively minor differences, the time budgets of the sexes (and, hence, their contributions to parental care) are approximately equal in shorebirds (Gibson 1978, Miller 1985, Gratto-Trevor 1991).

Walters (1982, 1984) proposed a framework for explaining variation in parental behavior

among and within species of shorebirds based on characteristics of the breeding habitat. "Active" tending involves following chicks and gathering them by calling to keep them nearby, whereas "inactive" tending involves stationary adults that only occasionally move to a new position near their chicks (Walters 1982). According to this model, species (and populations within species) in largely open habitats with abundant food are more likely to tend their young "inactively" because predators can be detected at greater distances, and the young do not wander as far in search of food and seldom become separated from their parents. In contrast, species living in habitats with lower visibility and less food should tend their chicks more actively because predator detection occurs when the predator is closer to the chicks, chicks must disperse farther to find food, and, as a result, the potential for chick mortality is higher. Habitat visibility, rather than predator abundance, is presumed to determine the nature of parental tending.

We studied Semipalmated Plovers (*Charadrius semipalmatus*) at Churchill, Manitoba, Canada. In this and other populations (Sutton and Parmelee 1955), plovers breed in two distinct

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locations, coastal and inland. Coastal habitats are open, food-rich, and the primary feeding area for adults is close to nesting sites. Inland habitats have lower visibility, less food in the adjacent ponds, and adults must fly up to 8 km between feeding and nesting sites (Rippin Armstrong and Nol 1993). Although each of these habitat features might result in different expectations of the appropriate parental behavior, the general differences (i.e. openness and food for chicks) are similar to those described by Walters (1984) for three species of lapwings (*Vanellus* spp.), which have similar foraging and parental behavior to *Charadrius* plovers.

Given the potential for variation in parental behavior between the sexes, and variation in breeding habitats, our study had two objectives. First, we determined whether the sexes differed in their contribution to parental care and in their temporal pattern of incubation. We predicted that, as in other socially monogamous shorebirds, the contribution to parental care by each sex would be about equal. Second, we tested whether parental behavior differed as a function of the degree of visibility and the amount of food in the breeding habitats. We predicted that in the more open, coastal locations, parents would exhibit fewer vigilant behaviors while incubating. During chick rearing, we predicted the same patterns of vigilance as during incubation and also that distances between adults and young would be shorter at more enclosed inland sites than at coastal sites because long-distance visibility is diminished and food for the chicks is sparse. We also tested the prediction that chicks at inland sites would be more dispersed where food is sparse. We tested the predictions for the effect of sex and habitat on parental behavior by observing incubating parents and parents attending chicks in both locations.

METHODS

We studied Semipalmated Plovers on the west coast of Hudson Bay near Churchill, Manitoba (58°45'N, 94°04'W) during the breeding seasons of 1992 and 1993 as part of a long-term study on this species (see Rippin Armstrong and Nol 1993). At least one adult from each pair was banded with numbered aluminum bands and plastic color bands. Sexes were identified based on the amount of white in the supercilary stripe and the amount of black in the auricular patch, with males having significantly less white and more black than females (Cram and Sim-

mons 1981). Sexes display a mixed pattern of dimorphism; females are heavier than males but have shorter tarsi and bills (Teather and Nol 1997).

Semipalmated Plovers lay a clutch of four eggs in a depression on the ground. They nest primarily on gravel areas but occasionally (2 to 5%) on tundra, mudflats, or forest edges. The size of the gravel nesting areas did not differ at coastal and inland locations, although the surrounding vegetation differed (Rippin Armstrong and Nol 1993). Coastal habitats consisted of extensive gravel and shale with small patches of low-lying willow (*Salix* spp.) and birch (*Betula glandulosa*) on the edges of the gravel expanses. Inland, the gravel areas were surrounded by willows (*Salix* spp.), birches (*Betula* spp.), white spruce (*Picea glauca*), and tamarack (*Larix laricina*). In addition, chicks in coastal locations could easily reach the coastal mudflats to forage, whereas chicks in inland locations generally foraged in small freshwater ponds (Rippin Armstrong and Nol 1993). Hatching success between the two sites varied between years but was not consistently higher at one or the other site (Nol unpubl. data).

We recorded distances between nest sites and the nearest foraging sites for each pair. The percent visibility surrounding each nest was recorded by estimating the amount of obstructed view at 1, 2, 5, and 20 m around the nest (Metcalf 1984). In 1993, visibility at 50 and 100 m also was estimated by placing a plover-sized fluorescent-pink object in each nest. While kneeling at a height of 1 m from the ground (to approximate the visibility of the nest to terrestrial predators), we recorded the percent of the object that was visible. Visibility at each nest was estimated in four directions, and an average visibility for each nest was calculated. Avian predators included Rough-legged Hawks (*Buteo lagopus*), Northern Harriers (*Circus cyaneus*), Merlins (*Falco columbarius*), Parasitic Jaegers (*Stercorarius parasiticus*), Herring Gulls (*Larus argentatus*), Short-eared Owls (*Asio flammeus*), and Common Ravens (*Corvus corax*). Gulls and ravens were considered to be the main potential predators of eggs, whereas the other species were considered to be potential predators of adults and young.

To determine whether food abundance differed between the two locations, we collected aquatic invertebrates with a core sampler (diameter of 11.0 cm and depth of 2.5 cm) at randomly selected locations in known feeding areas of plovers. Half of the soil core (108 cm³) was sifted, and the invertebrates were identified to order and counted. Samples were collected every three days at four coastal and inland sites during and before laying and at three coastal and inland sites during chick rearing. Based on previous studies of collected individuals (Baker 1977, Michaud and Ferron 1990, Napolitano et al. 1992), we assumed that polychaetes, dipteran larvae, oligochaetes, nematodes, and trichopterans were poten-

tial prey items. One of three plovers collected on the coast near Churchill in 1992 had an empty stomach, and the other two had 32 and 108 polychaetes in their stomachs, respectively (pers. obs.). Semipalmated Plovers probably are flexible in their choice of prey. We assumed that differences in quantity of prey between sites were more important than differences in prey species composition (see Skagen and Oman 1996).

In 1992, we observed incubation behavior for short periods only and did not include these observations in our results. In 1993, we conducted systematic observations of incubating parents. Observation periods lasted 4 h and were conducted three times at each nest during the incubation period: (1) days 1 to 8 of incubation, (2) days 9 to 16, and (3) days 17 to 22. Nests that were depredated before the third observation period were replaced with another nest at the same site. Because the birds nested very synchronously (Nol et al. 1997), replacement nests usually were at the same stage as depredated nests. Adults were observed during one to three observation periods over the chick-rearing period in both years. Observations during incubation and chick rearing were made using a 25 \times spotting scope; data were entered into a laptop computer using a BASIC program (written by C. Risley) that recorded the duration and frequency of each behavior. During nocturnal watches we determined the sex of incubating individuals before darkness fell and could detect when a bird relieved its mate, even during the darkest hours (0000 to 0200 CDT). Because the results were similar for duration and frequency data for all statistical comparisons (Sullivan Blanken 1996), we report detailed analyses of frequency comparisons, although we report the average duration for the most common activities in each stage.

We classified the behaviors into "parental" and "somatic" activities (Brunton 1988a, b), roughly equivalent to active and inactive tending of Walters (1984). For incubating birds, we assumed that "alert," "look," and "tilt" were indicators of greater vigilance at the nest, whereas "peck," "preen," "head-in-wing," and "relax" were indicators of less vigilance. During chick rearing, we observed tending as well as nontending adults and categorized "alert," "brood," "look," "tilt," and "chase" as parental behaviors, and "walk," "peck," "preen," "stand/sit," "forage," "head-in-wing," and "relax" as somatic activities. Behaviors that we could not categorize easily as either parental or somatic included "fly" and "move" (on nest or with chicks). Components of the above categorizations included *Alert*: head extended, eyes wide open and bird scanning the area; *Brood*: chicks warmed by a parent; *Head down*: head held down and extended forward close to the ground, eyes wide open (incubation only); *Fly*: bird flies away from nest, usually due to a predator or a nest change; *Head bob*: bird lifts head and lowers

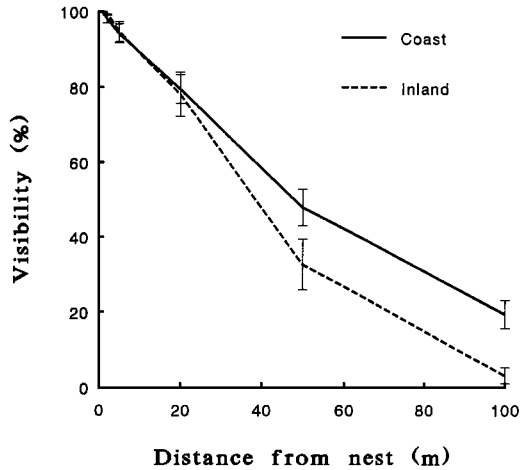


FIG. 1. Visibility as a function of distance from nest for Semipalmated Plovers nesting at coastal and inland locations. Repeated-measures ANOVA, distance \times location interaction, $F = 3.41$, $df = 5$ and 195, $P < 0.006$.

it quickly in succession; *Sit*: bird sits on territory near chicks; *Walk*: bird walks around territory; *Look*: bird is either scanning the horizon slowly or has its head held up but not extended and its eyes open; *Peck*: bird pecks at nest material or at the sides of nest cup; *Preen*: bird scratches or preens feathers; *Stand*: bird stands near nest or chicks; *Tilt*: bird tilts head toward sky, scanning; *Vocalize*: any vocalization produced by the bird; *Head-in-wing*: bird resting with eyes partly closed or not closed and with head behind wing in a sleeping posture; *Relax*: bird's head held in a relaxed position and eyes slightly closed; and *Chase*: adult chases another bird away from eggs or chicks. Simultaneous behaviors were scored twice (e.g. a bird that called while chasing was tallied as a "chase" and a "vocalize").

We estimated distances between attending parents and their chicks. The average distance of all chicks from each brood, at each age, was used in analyses. During observations of incubating or tending adults, we also recorded the approximate distance at which plovers appeared to react to a predator overhead.

RESULTS

General biology and habitat differences.—Semipalmated Plovers in Churchill begin egg laying in June. Most chicks hatch by mid-July, and all chicks have fledged by mid-August (Rippling Armstrong and Nol 1993, Nol et al. 1997). Visibility was significantly higher at the coast than inland at long distances from the nest (100 m) but not closer (Fig. 1). The distance to nearest

suitable foraging sites for chicks did not differ significantly between locations (coast: $\bar{x} = 3.95 \pm \text{SE of } 0.21 \text{ m}$, $n = 26$; inland: $\bar{x} = 4.58 \pm 0.30 \text{ m}$, $n = 15$; $t = -1.76$, $P = 0.09$), a result consistent with earlier data (Rippin Armstrong and Nol 1993). Temperatures recorded throughout the study periods at coastal sites were consistently lower than at inland sites, but averaged less than 1°C lower, a difference that we considered minor (Sullivan Blanken 1996).

During chick-rearing periods, the median number of food items per core sample was significantly higher at coastal sites than at inland sites (coast: 131.1, range 15.5 to 945.1, $n = 3$ [mean of 5 to 6 samples per site]; inland: 4.7, range 4.1 to 6.5, $n = 3$; Mann-Whitney U -test, $P = 0.025$). The composition of prey was very different at the two locations ($G = 4,424$, $P < 0.0001$), with polychaetes dominating coastal locations and dipteran larvae dominating inland locations. At the coast, 94% of 168,138 invertebrates sampled were polychaetes, 5.6% were dipteran larvae, and 0.6% were nematodes; at inland sites, 40% of 555 invertebrates sampled were dipteran larvae, 29.5% were oligochaetes, 28.6% were nematodes, and 1.96% were trichopterans.

Incubating and chick-rearing plovers reacted to the presence of Herring Gulls by crouching on the nest and to other potential predators by running off the nest. We saw 124 aerial predators during 276.4 h of observation during incubation (88.7% of total) and only 16 aerial predators during 139.5 h of observation during the chick-rearing period (11.3%). During incubation, almost twice as many aerial predators were seen at coastal locations than at inland locations (79 vs. 45; $G = 10.48$, $P < 0.01$). During incubation and chick-rearing, terrestrial predators such as foxes (*Vulpes vulpes* and *Alopex lagopus*) were seen only occasionally, although at both locations the presence of fox tracks and observations of foxes near nest sites indicated that plovers and/or their eggs may have been lost to these predators.

Reactions (e.g. alert, vocalize, run off nest, etc.) by adults to potential predators of eggs occurred at a closer distance to the nest than reactions to potential predators of adults (egg predators: median = 18.3 m, range 0 to 98.3 m; adult predators: median = 50 m, range 0 to 225 m; Mann-Whitney U -test, $P = 0.03$). For neither category of predators was there a significant

difference in the reaction distance between coastal and inland sites (coast, egg predators: median = 15 m, range 0 to 98.3 m; coast, adult predators: median = 50 m, range 0 to 225 m; inland, egg predators: median = 34.8 m, range 10 to 63.8 m; inland, adult predators: median = 65 m, range 35 to 103 m; Mann-Whitney U -tests, $P_s > 0.05$ for both locations).

Incubation behavior.—We observed 23 nests for a total of 276.4 h. Both parents incubated almost equally, but in five continuous observation periods that spanned 0000 to 0530, males were on the nest during the darkest hours (0000 to 0200), and females were on the nest during the next 3 to 4 h (0200 to 0530). In four of these five observation periods, males incubated from 2230 to 0215 (in the fifth, we have no observations from 2230 to 0013, but the male was incubating between 0013 and 0215). The length of the incubation shift (averages from different females analyzed) was not affected by location ($F = 1.55$, $df = 1$ and 20, $P = 0.23$). Females incubated for shorter shifts than males, and nocturnal shifts (2200 to 0630) were more than twice as long as daytime shifts (sex effect: $F = 3.64$, $df = 1$ and 20, $P = 0.07$; time-of-day effect: $F = 30.0$, $df = 1$ and 20, $P = 0.0001$; female day: $\bar{x} = 98.4 \pm 15.17 \text{ min}$, $n = 8$; female night: $\bar{x} = 247.8 \pm 30.39 \text{ min}$, $n = 5$; male day: $\bar{x} = 136.0 \pm 20.61 \text{ min}$, $n = 8$; male night: $\bar{x} = 321.1 \pm 52.32 \text{ min}$, $n = 3$; analysis on log-transformed data).

Parents spent the greatest amount of time during incubation in the look behavior, followed by relax and head-in-wing; the frequency of these behaviors was not significantly different between locations (Table 1). During incubation, parents on the coast exhibited significantly fewer vigilant behaviors than inland parents (Table 2). Inland adults vocalized more (but not significantly so) than coastal adults during incubation. The total number of vigilant behaviors performed also was significantly lower at coastal than at inland sites. There were no differences between the sexes for any incubation behavior at either location.

Chick-rearing behavior.—During chick rearing, we observed one or both parents of 25 broods for a total of 139.5 h. Parents had similar time budgets at the coast and inland and spent about the same amount of time brooding chicks as they did standing near chicks and looking (Table 3). They also spent about equal amounts of

TABLE 1. Percent of total time ($\bar{x} \pm SE$) spent by adult Semipalmated Plovers in major behaviors during incubation at coastal and inland sites. No significant differences occurred when each behavior was tested for effects of sex and location (Friedman's two-way ANOVA).

Behavior	Males	Females
Coast		
Look	41.5 ± 2.1	49.3 ± 2.0
Relax	28.1 ± 2.9	24.8 ± 3.0
Head-in-wing	19.0 ± 3.1	10.3 ± 3.1
Other	11.4 ± 3.4	15.6 ± 2.6
<i>n</i>	16	14
Inland		
Look	42.4 ± 3.1	43.5 ± 2.5
Relax	33.1 ± 4.4	25.8 ± 2.4
Head-in-wing	12.3 ± 2.8	17.5 ± 3.8
Other	13.2 ± 2.7	12.2 ± 3.5
<i>n</i>	9	9

time vocalizing (alarm calls and calls to gather chicks) and foraging near chicks. For the frequency data, we found no significant location effects for any behavioral category (Table 4). Males vocalized and flew more than females at both locations (Table 4), but the number of times they exhibited parental versus somatic behaviors was similar.

Distances between adults and their chicks did not differ significantly between coastal and

TABLE 2. Frequency per h ($\bar{x} \pm SE$) of activities of incubating male and female Semipalmated Plovers.

Behavior ^a	Males	Females
Coast		
Vigilant ^b	29.4 ± 3.5	23.1 ± 3.7
Not vigilant ^c	38.7 ± 6.3	21.3 ± 4.9
Fly	0.3 ± 0.8	0.4 ± 0.3
Move	3.1 ± 0.5	2.9 ± 0.5
Vocalize	2.7 ± 0.7	2.1 ± 1.4
Out of view	1.6 ± 0.4	1.9 ± 0.4
<i>n</i>	16	14
Inland		
Vigilant ^b	34.7 ± 4.3	32.7 ± 4.3
Not vigilant ^c	27.5 ± 4.3	36.1 ± 7.0
Fly	0.2 ± 0.1	0.7 ± 0.6
Move	3.1 ± 0.4	4.3 ± 1.3
Vocalize	10.9 ± 7.1	11.9 ± 10.9
Out of view	2.1 ± 1.0	2.0 ± 0.7
<i>n</i>	9	9

^a See Methods for definition of vigilant and non-vigilant behaviors.

^b Significant location effect (Friedman's two-way ANOVA, $P < 0.05$).

^c Significant interaction effect (Friedman's two-way ANOVA, $P < 0.05$), but no significant main effects.

TABLE 3. Percent of total time ($\bar{x} \pm SE$) spent by adult Semipalmated Plovers in major behaviors during chick rearing at coastal and inland sites. No significant differences occurred when each behavior was tested for effects of sex and location (Friedman's two-way ANOVA).

Behavior	Males	Females
Coast		
Brood	36.6 ± 8.6	34.1 ± 8.4
Look	28.0 ± 5.5	36.3 ± 8.1
Vocalize	9.3 ± 3.3	8.1 ± 2.7
Forage	10.5 ± 2.3	6.1 ± 2.9
Other	15.6 ± 3.2	15.4 ± 2.7
<i>n</i>	15	12
Inland		
Brood	30.9 ± 9.4	32.0 ± 8.2
Look	32.1 ± 9.1	29.5 ± 6.8
Vocalize	10.6 ± 3.0	12.7 ± 4.4
Forage	10.1 ± 2.5	8.5 ± 3.9
Other	18.9 ± 2.5	14.7 ± 3.4
<i>n</i>	9	10

inland locations ($F = 1.02$, $df = 1$ and 44 , $P > 0.05$). As the chicks became older, however, adult-chick distances increased significantly (data combined for both locations; $F = 4.22$, $df = 18$ and 44 , $P < 0.0001$; Fig. 2). We also compared maximum distances between chicks (less than five days old) to determine whether chicks at inland locations with less food were more

TABLE 4. Frequency per h ($\bar{x} \pm SE$) of activities of male and female Semipalmated Plovers attending chicks.

Behavior ^a	Males	Females
Coast		
Parental	29.1 ± 5.5	30.3 ± 7.0
Somatic	37.7 ± 19.6	23.9 ± 4.7
Vocalize ^b	36.9 ± 15.0	24.8 ± 8.9
Walk	14.3 ± 6.4	12.8 ± 4.2
Fly ^b	3.3 ± 0.6	1.4 ± 0.4
Forage	2.9 ± 0.8	29.6 ± 18.1
Move	0.4 ± 0.4	0.4 ± 0.3
<i>n</i>	15	12
Inland		
Parental	29.0 ± 11.1	47.8 ± 11.6
Somatic	29.9 ± 14.6	10.7 ± 2.9
Vocalize ^b	57.2 ± 22.0	21.3 ± 8.6
Walk	14.0 ± 8.0	6.5 ± 2.3
Fly ^b	1.4 ± 0.8	0.5 ± 0.2
Forage	2.6 ± 0.6	2.2 ± 0.8
Move	0.8 ± 0.6	0.7 ± 0.7
<i>n</i>	9	10

^a See Methods for definition of parental and somatic behaviors.

^b Significant effect of sex (Friedman's two-way ANOVA, $P < 0.05$). No location effects were significant.

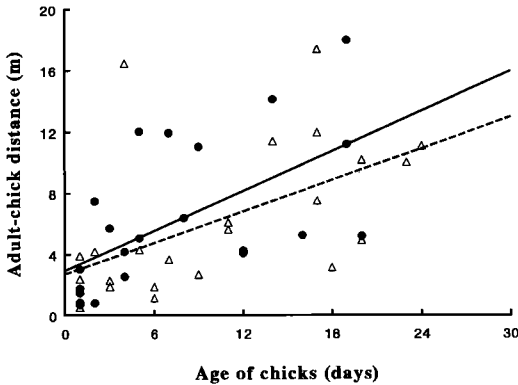


FIG. 2. Distance from active tending adult Semipalmated Plover to its chicks as a function of chick age and location. Coast (circles and solid line): distance = $0.43(\text{age}) + 2.96$; $r^2 = 0.35$, $P = 0.004$. Inland (triangles and dashed line): distance = $0.34(\text{age}) + 2.72$; $r^2 = 0.29$, $P = 0.008$.

dispersed than at coastal locations. Chicks at inland locations (median = 27.2 m, range 5 to 100, $n = 5$ broods) were more dispersed than chicks at coastal locations (median = 5.16 m, range 2.8 to 14, $n = 5$ broods; Kruskal-Wallis test, $\chi^2 = 3.27$, $P = 0.072$).

Adults brooded chicks during the first few days after hatching but rarely after chicks reached five days of age (Fig. 3). The amount of time adults spent brooding chicks did not differ between habitats. There was, however, a significant negative relationship between the amount of time spent brooding during the first five days and temperature (recorded between 0900 to 1200, $r_s = -0.35$, $n = 31$, $P = 0.05$, range in temperatures 5.25 to 19.0°C, 1993 data only; ANCOVA, temperature effect: $F = 5.81$, $df = 1$ and 37, $P = 0.02$; location effect: $F = 1.17$, $df = 1$ and 37, $P = 0.27$). Foraging by adults increased significantly as chicks became older, whereas alert activities and vocalizing did not change over the course of the parenting period (Fig. 3).

DISCUSSION

Sexual differences in parental behavior.—Time budgets of Semipalmated Plovers showed very little intraspecific variation. This is similar to findings for Least Sandpipers (*Calidris minutilla*) and Semipalmated Sandpipers (*C. pusilla*) in several geographic areas (Miller 1985, Gratto and Cooke 1987). While both sexes attended

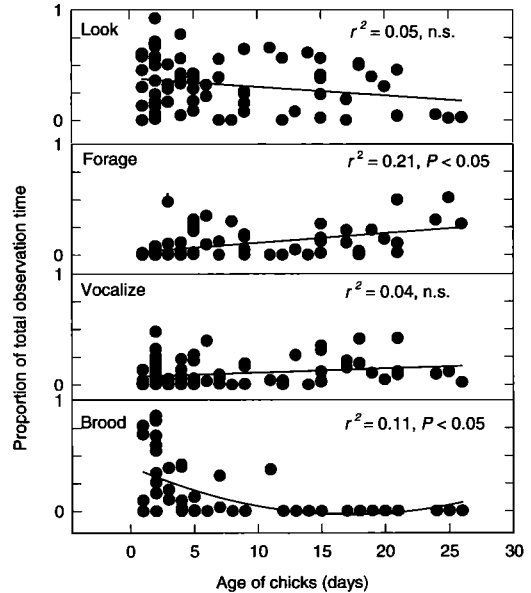


FIG. 3. Effect of chick age on the frequency of four chick-rearing behaviors. Each point represents an individual observed during a single observation period. All regressions are linear except for brooding, which is a negative exponential.

young, plovers incubated and brooded approximately equally, although males flew and vocalized more during chick rearing than did females. These results are very similar to those for other socially monogamous shorebirds with approximately equal contributions of the sexes to parental care (Gibson 1978, Cairns 1982, Mundahl 1982, Pienkowski 1984, Miller 1985, Nol 1985, Bergstrom 1986, Gratto-Trevor 1991). Greater feeding by females in the multiple-brooded Killdeer during late incubation probably functions to provide them with nutrients for subsequent clutches (Brunton 1988a). Semipalmated Plovers at Churchill rarely re-nest after losing the first nest (5 of 209 nests; Nol et al. 1997). Thus, feeding during chick rearing would not increase the probability of re-nesting.

Male-biased incubation during the darkest hours also is characteristic of Killdeers in temperate regions (Mundahl 1982, Warnock and Oring 1996). Female Semipalmated Plovers were very consistent in incubating for long shifts from 0200 to about 0600. Incubation rhythms during the daylight hours (between 0600 and 2200) did not appear to follow a regular pattern among pairs, possibly because disturbance by people, predators, and other birds

resulted in more frequent nest exchanges. Because female Semipalmated Plovers are slightly heavier than males (ca. 3.5%; Teather and Nol 1997), a greater ability of males to escape a surprise nocturnal attack by a predator (e.g. Gosler et al. 1995) may explain male-biased nocturnal incubation. Alternatively, if females have a greater energy deficit because of egg laying, they may benefit from nocturnal foraging when invertebrates such as polychaetes are most active (Robert and McNeil 1989).

Effect of habitat on behavior.—Coastal locations had greater horizontal visibility, higher food abundance for chicks, and, as a result, chicks were slightly less dispersed than at inland locations. During incubation, but not during chick rearing, aerial predators were more common on the coast than at inland sites. Our data indicate that potential predators of adults were detected at a greater distance than potential predators of eggs and/or chicks, but detection distances did not differ between habitats, despite differences in long-distance visibility between sites.

We had no quantitative estimates of the number of terrestrial predators, but the effects of predation by foxes, in particular, varied greatly from year to year. A high predation rate at one coastal site, at least in 1992, clearly was due to foxes. (Sullivan Blanken unpubl. data), but a high level of fox predation also has been recorded at inland sites (Rippin Armstrong and Nol 1993). Therefore, we assume that predation by terrestrial predators was approximately equal (and unpredictable) at inland and coastal sites, and only the horizontal visibility, and hence the ability to detect terrestrial predators, was important in potentially affecting the behavior of the parents. This relatively equal predation at the two sites was supported by data that show that neither coastal nor inland sites had consistently higher hatching or fledging success during six years of study (Nol unpubl. data).

Incubating parents at inland locations spent more time in vigilant activities that presumably functioned to detect predators. This behavioral difference was consistent with the lower visibility at long distances caused by surrounding trees and the higher probability of surprise by terrestrial (and possibly aerial) predators at inland locations. If these antipredator activities can be embraced into Walters'

(1984) categorization of "active tending," then these results are consistent with his model predicting that shorebirds nesting in more closed environments will exhibit more active tending than those inhabiting more open environments.

During chick rearing, the frequency of "parental" versus "somatic" behaviors did not differ between the two habitats. Unlike the findings for Southern Lapwings (*Vanellus chilensis*) in two environments (Walters 1984), parent-young distances in Semipalmated Plovers did not differ between habitats. Because young chicks at inland locations were more dispersed than chicks at coastal locations, inland parents may have been more vigilant to maintain the same distance from their chicks as parents at coastal locations—a behavior that could be considered a form of active tending (Walters 1984). During chick rearing, coastal parents chased other Semipalmated Plovers more frequently, probably because at coastal mudflats many broods were feeding simultaneously, and contact with conspecifics and other birds occurred more frequently.

Other factors influencing parental behavior.—We found a significant negative relationship between ambient temperature and the proportion of time parents spent brooding their chicks (see also Beintema and Visser 1989). As in Ringed Plovers (*C. hiaticula*; Pienkowski 1984), we predicted that the close proximity of food at the coast would result in more frequent nest changes because off-duty (i.e. nonincubating) parents would be able to relieve on-duty parents earlier, assuming that in both habitats nest exchanges were equally inconspicuous to predators. However, neither the number of changes at the nest nor the length of incubation bouts was different between the two habitats. Semipalmated Plovers change incubation duty at about the same frequency (ca. once per hour) as plovers at temperate latitudes (Killdeer, Nol 1980; Piping Plover [*Charadrius melodus*], S. Haig pers. comm.), but frequently compared with Wilson's Plover (*C. wilsonia*, Bergstrom 1986, Thibault and McNeil 1995) and Greater Golden-Plover (*Pluvialis apricaria*, Byrkjedal 1985), both of which change shifts about once every 12 h. In the case of Wilson's Plover, the risk of predation was thought to contribute to long incubation bouts (Thibault and McNeil 1995). Predation rates also can be very high (up

to 50% of nests) for Semipalmated Plovers in Churchill (Rippin Armstrong and Nol 1993, Nol et al. 1997). Thus, this reasoning does not seem to explain the long shifts in Wilson's Plovers. The conspicuous nature of Greater Golden-Plovers during nest exchanges may attract attention to the nest (Byrkjedal 1985), resulting in selection for longer incubation bouts. The evolution of the length of incubation bouts in shorebirds probably results from interactions among body size, degree of conspicuousness, climate, and energetics of incubating birds (see Cartar and Montgomerie 1987). The phenomenon is not well studied and deserves further attention.

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