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BI-PARENTAL CARE IN KILLDEER: AN ADAPTIVE HYPOTHESIS

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Parental care (here defined as investment made by adults in their young after hatching) occurs in all birds except the Megapodidae. It is to be expected that the amount and proportion of time and energy devoted to parental care will profoundly affect reproductive success. Furthermore, the strategy of parental care (whether young are tended by male, or female, or both) will have far reaching effects on the mating system (Lack 1968, Orians 1969). Participation of both sexes in parental care is widespread among birds and easily understood when the young are fed by their parents (Lack 1968). However, in several monogamous anatids, charadriids, scolopacids and recurvirostrids in which both adults tend precocial, independently foraging young, participation of both sexes in parental care is problematic (Selander 1972).

This paper discusses parental behavior of the monogamous Killdeer (*Charadrius vociferus*), in which broods may be tended by either 1 or 2 adults. To assess advantages of bi-parental care for a species with precocial young, I contrast time budgets for adult behavior with both parents and only 1 adult tending the brood and suggest hypotheses for strategies of parental care in this species.

Killdeer arrive in mid-March at my study area in St. Paul, Minnesota. Males often return to a previously occupied territory and in some instances retain the same mate (Lenington and Mace 1975). Courtship activities and pair formation begin immediately after arrival. Bunni (1959) did the only detailed study of Killdeer breeding biology. He reported a clutch-size of 4 and an incubation period of 24–26 days. Males and females participate equally in incubation. Occasionally Killdeer are double-brooded, with eggs for second nestings laid before the first brood has fledged. The young, never fed by their parents, fledge at about 31 days. If a clutch is destroyed, Killdeer may nest up to 3 times.

METHODS

This study was done in the 1972 breeding season on 150 acres on, and adjacent to, the Minnesota State Fair Grounds, where suitable Killdeer habitat was broken up by busy streets and large complexes of buildings (Fig. 1). Killdeer nested on areas with low or sparse vegetation and foraged regularly on lawns, the margins of ponds and the edges of a drainage ditch.

I watched 8 broods and 13 attendant adults. Five broods were tended by both adults and 3 by 1 adult. Eight adults, including at least 1 from each pair, were trapped and banded with

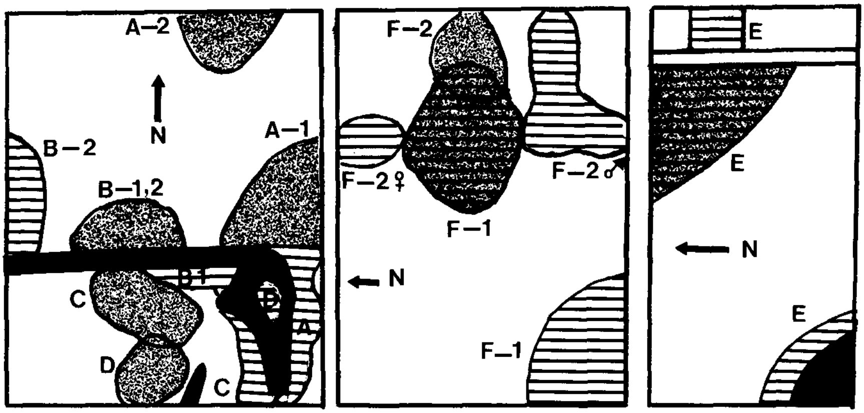

FIG. 1. Scale map of the study area. Scale: 1 in = 75 f. Gray areas are nesting territories, striped areas are feeding territories and solid black areas are standing water. Pairs are labled with letters. In the case of pairs that raised more than 1 brood, locations of individual broods are indicated with numbers (e.g., B-1 = the location of the first brood of pair B).

both colored and numbered Fish and Wildlife Service bands. Sex of adults was determined by the position assumed during copulation. Chicks were color-banded while still in the nest. All observations were made from a car or canvas blind using 7× binoculars and a 25× spotting scope. When recording data, adults in 2-parent broods were classified as either "attentive" or "non-attentive." The attentive adult was either the one that called, led, or brooded chicks, or the bird consistently closest to the chicks. Usually the non-attentive adult was far enough from the chicks to be easily determined. When it was impossible to decide which bird was attentive, both birds were called "attentive."

Estimates of the time budget for parental care were based on 158.3 h of observation, distributed as shown in Table 1. Observation periods for individual broods ranged from 1–5 h/day. The amount of time parents engaged in each of 10 activities was timed to the nearest ½ min. Of these activities, only "standing," "foraging," "anti-predator behavior," "aggression," "brooding" and "incubation" are discussed in this paper. The other 4 activities (calling chicks, preening, courtship and interspecific aggression, e.g., aggression toward Spotted Sandpipers (*Actitis macularia*) comprised less than 5% of the adults' time.

"Standing" consists of all standing, including any pause during preening or feeding of at least 30 sec, but not short pauses during aggressive or courtship activities. "Foraging" comprises all time a bird spent seeking and capturing prey. "Anti-predator behavior" includes giving alarm calls, standing in an alert posture or displaying (see Deane 1944 for a description of Killdeer anti-predator displays) to a potential predator. "Aggression" consists of chasing, fleeing and threat displays between conspecifics (see Phillips 1972 for a description of Killdeer aggressive displays). "Brooding" involves both brooding and shielding chicks from the sun. "Incubation" includes sitting on eggs.

Distances between a chick and the nearest observable chick, and between chicks and the attentive adult were recorded every 10 min. If chicks were in dense vegetation, distances between chicks and the attentive adult were noted whenever a chick became visible. When more than 1 chick emerged, the distance between them was noted. All measurements of distance are estimates based on known distances between landmarks.

TABLE 1
DISTRIBUTION OF OBSERVATION TIME

	Hours	Percent
Age of chicks		
Week 1	49.6	31.3
Week 2	33.9	21.4
Week 3	43.2	27.3
Week 4	17.7	11.2
Week 5	13.9	8.8
Total	158.3	100.0
Time of day		
Dawn–12:00	87.7	55.5
12:00–17:00	45.9	29.0
17:00–sunset	24.7	15.5
Total	158.3	100.0
Roles of adults		
Attentive adult 2-parent broods	98.0	61.9
Non-attentive adult 2-parent broods	35.3	22.2
Attentive adult 1-parent broods	25.0	15.9
Total	158.3	100.0

RESULTS

Hatching and leaving the nest.—Hatching dates on the study area in 1972 ranged from 15 May–22 July. Non-attentive adults were never seen on the territory as eggs were hatching, except during nest relief, or when the nest was threatened by a predator. Attentive adults brooded the chicks continuously during the first few hours after hatching. After chicks were about 6 h old they occasionally emerged from beneath the adult and stood by the nest for up to 15 min. Chicks remained at the nest-site throughout the day of hatching and the following night, after which they were led from the nest by the parents. Both adults accompanied the chicks as they left the nest. Neither adults nor chicks were observed to return to the nest-site.

Movements of the brood.—During courtship and incubation Killdeer defend both a nesting territory and 1 or more feeding territories. Seven of the 8 broods were taken to feeding territories and only 1 pair (pair E, see Fig. 1) remained with its brood on the nesting territory. Availability of cover was an important factor associated with where adults took chicks. Although 3 broods (E, F_1, F_2) used areas which lacked standing water, all

TABLE 2
PERCENTAGE OF OBSERVATION TIME EACH ADULT TENDED CHICKS AND PERCENTAGE OF TIME EACH SPENT TENDING CHICKS IN RELATION TO EGG-LAYING FOR 2 PAIRS

Brood	Minutes of observation	Percent[1]	
		Male	Female
B_1	1075	31.6	68.4
D	717	48.7	53.3
F	1607	44.0	56.0
A Pre-laying	704	30.4	69.6
Laying	303	80.5	19.5
Post-laying	610	45.0	55.0
E Pre-laying	1146	62.4	37.6
Laying	405	84.7	43.5
Post-laying	615	52.5	54.7
Laying of third clutch	314	64.0	45.1
Post-laying	1090	54.4	70.5

[1] The percentage totals are more than 100% as a result of instances in which both parents tended chicks.

broods were taken to areas where dense herbaceous vegetation was available; there chicks hid at the approach of a predator. Pair E had nested in an area with heavy herbaceous cover, whereas their 2 feeding territories had sparse vegetation. In this instance, the brood remained on the nesting territory even though the adults used the feeding territories for much of their own foraging.

All pairs continued to defend and occasionally use the original nesting territory until the chicks fledged. One pair (F) returned to the nesting territory to brood chicks at night. Other pairs returned to the nesting territory when the feeding territory was temporarily disrupted by flooding or human construction work. Finally, 5 of 6 clutches for second broods were laid on the original nesting territory.

Attentiveness and formation of 1-parent broods.—Chicks were only unattended when parents responded to a predator, were involved in aggressive encounters with other Killdeer, or were engaged in precopulatory displays or copulation. However, in 2-parent broods, normally only 1 adult at a time remained near the chicks. The non-attentive adult remained at least 23 m from the brood while chicks were young. After chicks were about 2 weeks old, non-attentive adults occasionally spent time near the brood and both parents sometimes tended the chicks. In general, attentive periods lasted 1–1½ h but varied considerably (range 10–327 min).

Females predominated in attentiveness in four 2-parent broods and males in 1 (Table 2). In the 2 (A, E) of 4 (A, B, E, F) second broods for

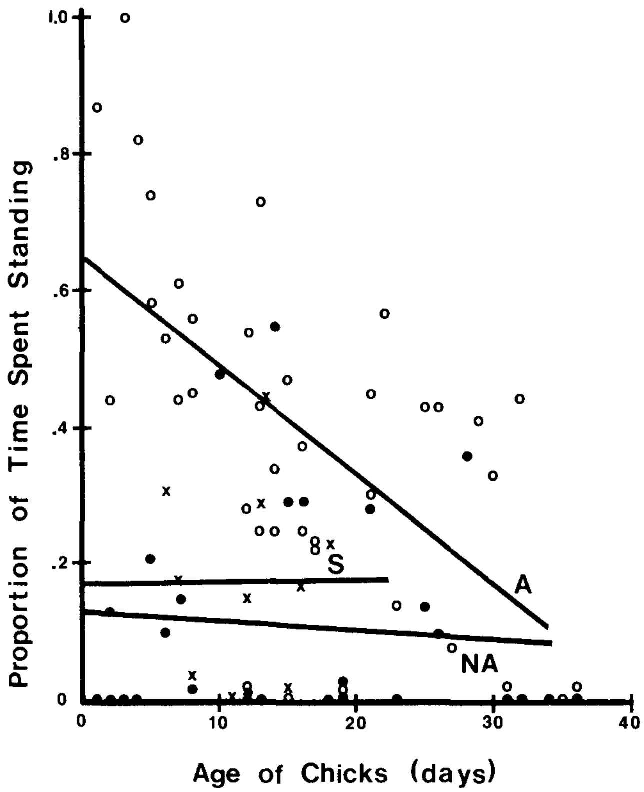

FIG. 2. Relationship between age of chicks and proportion of time adults spend standing. A = attentive adults in 2-parent broods; NA = non-attentive adults in 2-parent broods; S = adult in 1-parent broods. Open circles are observed points for A, closed circles are observed points for NA, and ×'s are observed points for S. Pearson's $r_A = -0.623$, $P < 0.05$; $r_S = +0.023$, NS; $r_{NA} = -0.245$, NS.

which I have adequate data, the proportion of time males tended chicks increased markedly from 1 day before the first egg was laid through the period of egg-laying. After eggs were laid, the proportion of time he tended chicks decreased.

There were no significant differences between attentive and non-attentive adults in the proportion of time spent incubating eggs for second broods ($t = 1.42$, df = 54, $P > 0.05$, N = 56) or in incubation time between males and females ($t = 0.93$, df = 54, $P > 0.05$, N = 56).

All first broods were tended by 2 adults. Two of the 4 clutches for second broods hatched and in each instance the second brood was at-

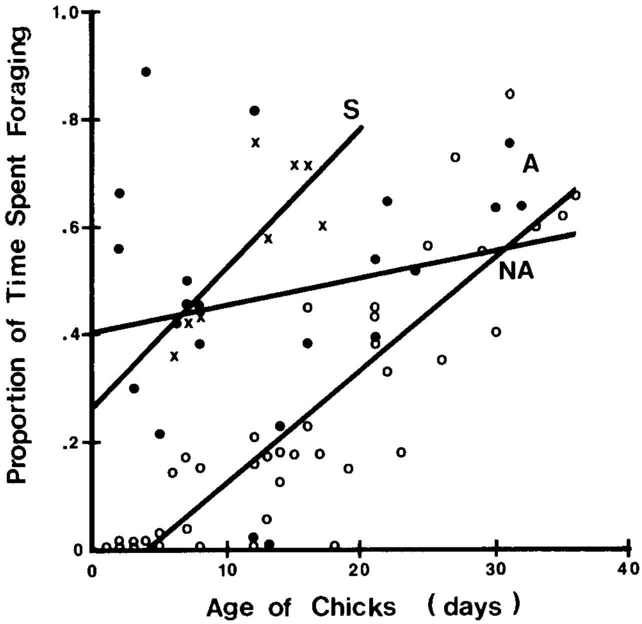

FIG. 3. Relationship between age of chicks and proportion of time adult spent foraging. Symbols are the same as in Fig. 2. Pearson's $r_A = +0.874$, $P < 0.01$; $r_S = +0.777$, $P < 0.05$; $r_{NA} = +0.207$, NS.

tended by only 1 adult. In the first case (B) the female left her second brood when the chicks were 6 days old and the male cared for the chicks until fledging. In the second case (F), the parents divided the brood sometime between 7 and 10 days after hatching. Each adult took 1 chick (the other 2 chicks disappeared during the first 5 days after hatching) and moved about 100 m apart. The brood remained separated day and night and no further interaction between the adults was observed. On the twelfth day after hatching, the banded male developed a lame foot. On the thirteenth day he had frequent aggressive encounters with an unmarked bird; the next day an unmarked bird assumed care of the chick in the area previously defended by the male. The foster parent brooded the chick and behaved in every way like a normal attentive adult.

Time budget.—Standing was the predominant activity of attentive adults in 2-parent broods while chicks were young (Fig. 2). While standing attentive adults usually faced their chicks. As chicks grew older, standing by attentive adults decreased markedly. Non-attentive adults and adults in 1-parent broods spent relatively little time standing; the time spent standing did not appear to change with the age of the chicks.

TABLE 3
THE DISTRIBUTION OF DEFENSE TIME BETWEEN ATTENTIVE (A) AND NON-ATTENTIVE (NA) ADULTS IN 2-PARENT BROODS

Age of chicks (weeks)[1]		Predators		Conspecifics	
		A	NA	A	NA
1	min	66	113	54	74
	%	36.9	63.1	42.1	57.8
2	min	17	20	41	11
	%	46.0	54.0	78.8	21.2
3	min	37.5	0	179	28.5
	%	100.0	0.0	86.5	13.5
4	min	51.5	0	15	0
	%	100.0	0.0	100.0	0
5	min	17	0	42	4.5
	%	100.0	0.0	91.3	8.7

[1] The first 3 weeks of observations are based on 4 broods and the last 2 weeks on 1.

The relationship between foraging time of adults and the age of their chicks is shown in Fig. 3. In 2-adult broods, Killdeer rarely fed while tending young in the first 2 weeks after hatching. Foraging occurred only when adults were non-attentive. Attentive adults and adults in 1-parent broods fed more as their chicks grew older. An analysis of covariance on the regression lines for attentive adults and adults in 1-parent broods showed no significant difference in the slopes ($t = 0.55$, df = 46, $P > 0.05$, N = 48), but there was a significant difference in the intercepts ($t = 17.02$, df = 46, $P < 0.001$, N = 48). Adults in 1-parent broods foraged more than did attentive adults in 2-parent broods, since adults in 1-parent broods can only forage while near their chicks; they have no "off duty" time. Non-attentive adults spent about 40% of their time foraging. The proportion of time they devoted to feeding did not significantly increase as the chicks grew older.

During the first week after hatching non-attentive adults defended the chicks against conspecifics and predators (Table 3), while the attentive adult stood near and faced the brood. When chicks were about 1 week old, attentive adults increasingly defended territory and brood. By the third week after hatching they performed virtually all the defense.

Only 1 adult at a time was ever observed brooding chicks. Chicks were brooded frequently for 2 days after hatching, but much less frequently after that. During rain they were brooded up to 15 days old and at night up to 18 days old.

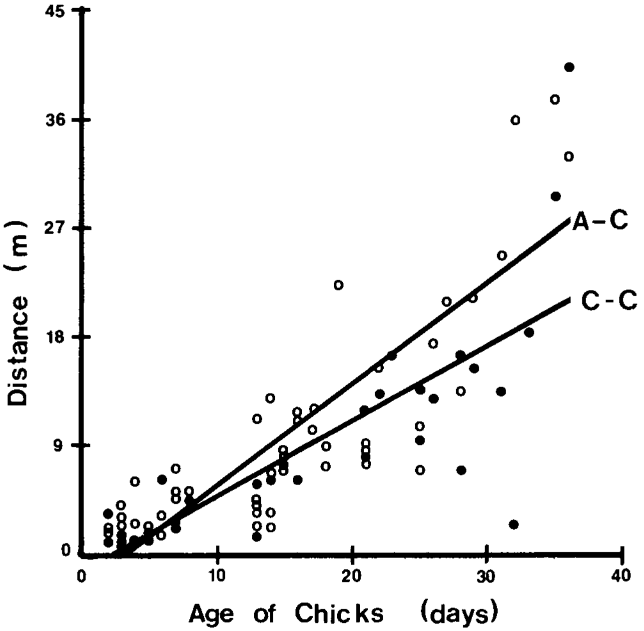

FIG. 4. Relationship between age of chicks and distance between birds. A–C = adult–chick distance, C–C = distance between a chick and the nearest chick. Open circles = observed points for A–C, closed circles = observed points for C–C. Pearson's $r_{A-C} = +0.858$, $P < 0.01$; $r_{C-C} = +0.780$, $P < 0.01$.

Distance between birds.—The distance between attentive adults and chicks and between a chick and the nearest chick increased as chicks grew older (Fig. 4). During a 3-week period I noted the activity of attentive adults (whether feeding or standing) when recording distances between adults and chicks. Distances between adults and their chicks did not differ significantly as a function of adult activity.

Fledging period and breeding success.—Chicks fledged 29–34 days after hatching. Adults and fledged chicks stayed together on the feeding area for 3 or 4 days; families then broke up. I occasionally found adults and fledged chicks in flocks of Killdeer that gathered in late summer on the breeding area, but no further interactions between adults and their chicks were observed.

All broods were followed from egg-laying until chicks were lost or fledged. The number of pairs in this study, however, was too small to permit meaningful comparisons of breeding success for 1- and 2-parent broods. Fledging success for 2-parent broods was 1.2 chicks/pair (SD = ±0.98, N = 6), and 1.5 chicks/pair fledged from 1-parent broods (SD =

±0.71, N = 2). Overall fledging success was 1.6 chicks/pair (SD = ±1.03, N = 6).

DISCUSSION

Four hypotheses for the evolution of bi-parental care in species with precocial young are: (1) two adults may be needed to brood chicks, especially as chicks mature; (2) two adults may detect predators sooner than one (Lack 1968); (3) two adults may be needed to defend the brood from predators or the territory from conspecifics (Pitelka et al. 1974); (4) two adults may be needed to prevent chicks from getting lost.

The data obtained in this study do not support the first hypothesis. Only a single adult was ever observed brooding chicks and thus 2 adults are not required for that purpose.

I have no data bearing directly on the second hypothesis, although it seems a likely factor favoring bi-parental care. This hypothesis could be tested by observing which adult gives the first alarm call when a predator approaches. If the first alarm call is most frequently given by the non-attentive adult, or alternatively, randomly distributed between the 2 adults, support would be provided for the predator detection hypothesis.

My data are insufficient to either confirm or reject the third hypothesis. In 2-adult broods most of the defense was performed by 1 adult alone. Two adults, however, were occasionally involved in defending broods against severe threats. Furthermore, it may be advantageous for adults to reduce individual stress by sharing defense.

Although the second and third hypotheses are probable factors favoring the evolution of bi-parental care, they do not account for the behavior of adults in 2-parent broods, particularly the considerable time adults spend standing near the brood. It is possible that the standing adult is watching for predators, but 3 kinds of evidence suggest other factors are also involved in this behavior.

(1) Adults spend less time standing and more time feeding as chicks get older, even though chicks probably remain vulnerable to predators until capable of sustained flight.

(2) When a predator approaches, the attentive adult often stands near the brood, rather than engaging in active defense. This behavior could potentially direct the predator's attention to the location of the chicks.

(3) Attentive adults usually orient toward the chicks. Since predators may approach from any direction, adult orientation should be random with respect to chicks, if the purpose of standing is to watch for predators. Instead, the orientation of adults suggests that the chicks themselves are being watched.

It is possible that highly mobile, precocial chicks need to be closely watched to prevent straying—the fourth hypothesis for parental care. Lost chicks are commonly reported for species with precocial young (Graul 1975, McBride et al. 1969, Parmelee et al. 1968, Ridpath 1971). In this study young chicks frequently wandered from the family group and seemingly did not respond to parental calls until the adult approached closely. One 5-day-old chick in my study did get lost. Both parents were displaying to a dog that had come near the brood. Despite frequent parental alarm calls, the chick got up from where it had been crouching, walked about 60 m from view, and was not seen again.

As chicks grow older they may be less apt to get lost, either because they have learned the boundaries of the adult's territory, or because as their nervous system matures they are better able to attend to parental calls. Few data are available on developmental changes in shorebird chick's responsiveness to parental vocalizations. However, studies of both wild and domestic populations of ducks (*Anas* spp.) and chickens (*Gallus*) have shown considerable individual variation among young chicks in ability to respond to parental calls (Collias and Collias 1956, Gottleib 1961, Jaynes 1956, Slucken 1964), despite the selective advantage of such behavior. In addition, both behavioral (Bateson 1964, Kaufmann and Hinde 1961) and neurological (Corner et al. 1966, Tuge et al. 1960) evidence indicates older galliform chicks sustain avoidance responses longer than younger chicks, suggesting that older Killdeer chicks may "freeze" longer than young chicks when parental alarm calls are given. Finally, both galliform and waterfowl young respond best to a combination of visual and auditory stimuli (Boyd and Fabricus 1965, Evans 1972, Porter and Stettner 1968) suggesting that adults may remain near young chicks to present a combination of visual and auditory cues.

If 2 adults stay with the brood, more time is available for watching chicks, since adults can feed while "off duty." In 1-adult broods all feeding must be done while tending chicks and consequently chicks are watched less. As the danger of chicks straying from the territory decreases, attentive adults in 2-parent broods are increasingly free to forage, or to defend territory and brood. Bi-parental care, however, usually persists until chicks fledge, suggesting that additional advantages, possibly related to defense or predator protection, accrue to 2-adult broods. If the above hypotheses are correct, bi-parental care should have a greater selective advantage than uni-parental care in Killdeer, and thus the existence of 1-parent broods requires explanation.

In Killdeer, uni-parental care has only been observed when second broods are raised (Bunni 1959). Bunni (1959) also reported that females always deserted their second brood, leaving near the time of hatching. In my study 1 of 2 second broods was deserted by the female and the other was split by the adults. Data from other shorebirds suggest that declining food late in the breeding season may be responsible for desertion of 1 adult from second broods. Sandpipers (*Calidris* spp., Holmes and Pitelka 1968) and Ruddy Turnstones (*Arenaria interpres*, Nettleship 1973) time nesting so that young hatch during the period of maximum food availability, and thus late second broods may hatch when food supply is diminishing.

Female desertion has been reported for several monogamous shorebirds, e.g., Lapwing (*Vanellus vanellus*), Green Sandpiper (*Tringa ochrops*), Common Sandpiper (*Actitis hypoleucos*) (Bannerman 1961); Great Knot (*Calidris tenurostris*) (Dement'ev et al. 1969); Stilt Sandpiper (*Micropalama himantopus*) (Jehl 1973); Greenshank (*Tringa nebularia*) (Nethershole-Thompson 1951); Ruddy Turnstone (Nettleship 1973); Dunlin (*Calidris alpina*) (Soikkeli 1967). Trivers (1972) suggests that the sex making the smallest parental investment is most likely to desert the young, since it has the least to lose. However, this argument has recently been criticized on theoretical grounds (Boucher 1977, Dawkins and Carlisle 1976, Maynard Smith 1977). No evidence was obtained in this study to support the hypothesis that females invested less in their young than did males. I found no significant differences between male and female behavior with respect to the first brood, nor in amount of time spent incubating the second clutch. Consequently, females probably invested more than males, since females produce eggs. Graul et al. (1977) and Maynard Smith (1977) have suggested that females will desert their young if they are so physiologically taxed after egg-laying that they are less able to raise the brood than are males. It may be, then, that female Killdeer desert second broods, not because they have invested less than their mates, but rather, because they have invested more.

SUMMARY

In order to assess the advantage of bi-parental care for Killdeer (a species with precocial young) I compared time budgets for adult behavior when both parents tended the brood with the time budget when only 1 adult tended the chicks. In 2-adult broods only 1 parent at a time remained near the brood and adults did most of their foraging while away from the brood. Thus adults in 1-parent broods fed more while near their chicks and watched their chicks less than did adults in 2-parent broods. The data suggest that predator protection and need to prevent chicks from straying from the brood are factors that may select for bi-parental care in this species.

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