Chapter 7

THE EVOLUTION OF PARENTAL BEHAVIOR AND CLUTCH SIZE IN SHOREBIRDS

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I. INTRODUCTION

In this chapter I consider two aspects of shorebird reproduction that are intimately related as components of life-history strategies: clutch size and parental behavior. That shorebirds with few exceptions do not feed their young, and that young are precocial, nidifugous, and relatively self-reliant, has led to the assumption that adults have little difficulty caring for their young. That is, it is generally assumed that parental care imposes few constraints on time and energy budgets of adult shorebirds (Kendeigh, 1952; Parmelee and Payne, 1973; Graul, 1973; Emlen and Oring, 1977; Welty, 1982, p. 293). This assumption has no empirical base, and data I collected from lapwings (Charadriidae, Vanellinae) indicate that parental care in fact imposes considerable demands on adults in at least some species. This justifies a reexamination of the parental care of shorebirds and of the assumption that clutch sizes are not limited by the ability of adults to care for young. This is further prompted by the lack of a satisfactory explanation of the limitation of clutch size in shorebirds.

In this context I present data on the parental behavior of lapwings, review parental behavior and clutch size in shorebirds generally, and consider the evolution of these components of life history within this group.

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II. PARENTAL BEHAVIOR

Parental care is defined as behavior directed by adults toward young that promotes the welfare of the young. Considering the volume of quantitative data on parental behavior collected from altricial birds, the absence of comparable data for precocial species like shorebirds is striking. These data are lacking because the things precocial birds do for their young (e.g., protect them from predators) are generally more difficult to quantify than is feeding young, the parental behavior most often measured in altricial birds. The difficulties of quantifying the cost of parental behavior to adults are magnified by the elusive behavior of adults with young, their habitation of environments in which observation is difficult, and their mobility. The lack of data is evident in Ricklefs' comparison of the energetic costs of reproduction in precocial and altricial birds over the various stages of the breeding cycle: only for the nestling stage of the precocial species was no estimate of energetic cost possible (Table 31 in Ricklefs, 1974).

A. Studies of Lapwings

Lapwings comprise a distinct subfamily of plovers containing 24 species (Bock, 1958; Morony et al., 1975). Most live in open habitats with short vegetation and are conspicuous, bold, and sedentary when breeding. Hence, they are more readily observed than most precocial species. The legendary alertness, aggressiveness, and incessant alarm-calling of these birds when breeding (Crawshay, 1907; Hudson, 1920; Wetmore, 1926; Archer and Godman, 1937; Jackson, 1938) indicate that parental care is well developed and natural history studies substantiate this (Bent, 1929; Laven, 1941; Skead, 1955; Hall, 1959, 1964; Jayakar and Spurway, 1965a,b, 1968; Little, 1967; Thomas, 1969; Barlow et al., 1972; Maclean, 1972a). Lapwings are thus ideal subjects for a quantitative analysis of parental behavior.

I studied four species of lapwings in order to (1) quantitatively document the forms that parental behavior takes and (2) obtain an estimate of the cost to adults of caring for young.

1. Methods

Study Areas and Populations. I studied lapwings at two sites. Long-toed Lapwings (Vanellus crassirostris), Blacksmith Plovers (V. armatus),
and Crowned Plovers (\textit{V. coronatus}) were studied in Amboseli National Park, Kenya (3°S, 37°E) during 14 months spanning 3 years (July–August 1975; August 1976–July 1977; December 1978). Southern Lapwings (\textit{V. chilensis}) were studied for 4 months (April–July 1978) near Mantecal, Venezuela (7°N, 69°W).

Amboseli is comprised of flat open savannah, with extensive short-grass plains, open \textit{Acacia xanthophloea} woodlands, and denser \textit{A. tortilis} woodlands. Although rainfall is seasonal and sparse (250–300 mm/year), permanent water is available at several waterholes and two large marshes (see Altmann and Altmann, 1970; Western, 1973). Mean daily temperature varies little from month to month in Amboseli (20°C to 25°C), but because of its elevation (1100 m), diurnal variation is large, typically about 20°C.

The Venezuelan site is a flat, open, seasonally flooded llanos, with scattered patches of forest and many small ponds. Open bajio and estero areas are especially common (see Ramia, 1967; Troth, 1979). The rainy season extends from April to October, and rainfall averages about 1500 mm/year. Mean daily temperatures are high, and vary relatively little monthly (24°C to 30°C). Diurnal variation is also slight, typically 10°C, due to the low elevation of the site (see also Eisenberg, 1979; Troth, 1979).

Demographic data and qualitative data on parental behavior were obtained by monitoring a local population of each species. For all species except Crowned Plovers, additional quantitative behavioral data were obtained by systematic observational sampling of a small segment (10–20 pairs) of the population (Walters, 1980).

**Behavioral Sampling.** No birds were banded, but adult Long-toed Lapwings and Southern Lapwigs were individually identifiable from slight variations in plumage. Neither species is sexually dimorphic, but sex could be determined from copulation position, which was consistent within pairs and has been shown to be a reliable indicator in a marked population of lapwings (\textit{V. miles}) in Australia (Barlow \textit{et al.}, 1972).

Time budgets and spatial relationships within families were estimated from scan samples (Altmann, 1974) of position and behavior taken 30 min apart. Each such sample included one or two pairs of lapwings and their young, and every few hours sampling was rotated among the 10–20 pairs observed. The behavioral categories used are defined in the Appendix. Approximately equal numbers of samples were collected during all daylight hours. Observations were made at close range from a vehicle that functioned as a blind, using binoculars.

The intersample interval is sufficient to ensure statistical independence of successive samples (Walters, 1980). Furthermore, because lapwings are highly visible and sedentary, individuals designated to be sampled were rarely out of sight. Estimates of time budgets and spatial relation-
ships are therefore relatively free of the biases that usually plague such estimates, and their accuracy is a simple function of sample size. Furthermore, breeding was asynchronous, so that all stages of the breeding cycle could be sampled simultaneously within a population. This greatly reduces confounding effects of seasonality on changes in behavior over the breeding cycle, simplifying interpretation of results.

Interspecific aggression and antipredator behavior were examined by focal sampling (Altmann, 1974) performed during the interval between scan samples. Samples were 10–20 min in duration, depending on species, and included one or two pairs. For all instances of these behaviors, the following were recorded: species of predator or intruder; behavioral response of lapwing adults and young to predator or intruder; effect of the lapwings’ response on the predator or intruder; distance between lapwing and predator or intruder when the response occurred.

Spatial relationships were examined by analysis of variance of interindividual distances using a square-root transformation (SPSS, Nie et al., 1975), and time budgets were compared by chi-square analyses of raw frequencies.

2. Parental Behaviors

I first briefly describe the parental behaviors observed and then in the following sections assess their benefits to young and costs to adults (see also Walters, 1980).

**Brooding.** Chicks were brooded frequently during the first week after hatching, and during inclement weather for several weeks thereafter. The frequency of brooding varied greatly among species according to weather conditions encountered during breeding. Brooding was most common in the Southern Lapwing, the only species that bred during the wet season.

**Antipredator Behavior.** Lapwings protected their young from predators by distraction displays, alarm calling, and aggression. Distraction consisted primarily of false incubation or running in a crouched posture while calling loudly; under extreme duress, Southern Lapwings performed an injury-feigning display. Swooping was the primary form of aggression, whether predators were on the ground or in the air.

The general antipredator behavior of lapwings was to detect dangerous predators, induce a response from their young through communicatory behavior, and provide additional protection of young through predator-directed behaviors. Within this framework there was complex variability. Alarm calls were complex, perhaps forming a graded series. Furthermore, adult response varied in consistent ways with species, location, and behavior of the predator, and with stage of lapwing breeding
cycle. The patterns evident in the more than 400 encounters with potential predators sampled indicate that adults have sophisticated discriminatory abilities, and may even be able to evaluate the danger to young inherent in each encounter with a potential predator and respond appropriately (Walters, 1980). For example, adults responded to falcons and harriers (Circus sp.) when these predators were still far away (typically > 100 m), but ignored vultures, snail-eating kites, and fish-eating raptors unless they were within a few meters of the young. Southern Lapwings emitted alarm calls in response to avian and mammalian predators that caused young to crouch and remain motionless, but emitted a much different alarm call in all 11 observed encounters with reptilian predators, and it caused the young to flee and remain upright. Certain species of potential predator evoked responses only during particular stages of the breeding cycle and were ignored during others. What is known of the behavior and diets of the various predators and the consequences of the various antipredator behaviors suggests that the variation in response to predators by lapwings is functional, i.e., it reflects the degree and kind of danger represented by the predator (Walters, 1980).

**Interspecific Aggression.** The selectivity, location, and timing of aggression by lapwings toward other species of birds intruding on their territories indicated that such aggression was a form of parental behavior (Walters, 1979, 1980). Such aggression was most frequent when young were present, and was associated spatially with the young. The mean frequency of interspecific aggression by lapwings tending downy chicks ranged from 3 to 20 attacks per pair per hour, depending on species.

**Vigilance.** Vigilant behavior, i.e., alert and rest-alert behavior (Appendix), was strongly associated with the presence of young, although it occurred infrequently in other circumstances (see below). Vigilance was directed both toward the young and toward the environment.

**Foraging Away from Young.** Adults moved away from their young to forage. This avoidance of young was specific to foraging, but was neither a necessary consequence of the nature of foraging nor a reflection of differences in microhabitat preference. I therefore interpret avoiding foraging near young as a parental behavior.

The specificity of the avoidance is evidenced by data on interindividual distances. Adult Long-toed Lapwings foraged far from downy young, but nonforaging adults stayed close to young regardless of chick behavior (Fig. 1). Adults ceased foraging away from young as the young matured, and eventually were as near to them when foraging as when not foraging. (Other parental behaviors waned with chick age similarly; see below.) Neither did adults forage away from their mates when young were not present (Fig. 1).
Fig. 1. Distance between adult Long-toed Lapwings and their young as a function of adult behavior and stage of the breeding cycle. Values are given for both foraging (F) and loafing (R: resting, sitting, or preening) adults. Stages of the breeding cycle are identified according to the development of the young. Downy plumage persisted for 3 to 4 weeks after hatching (DOWNY stage) until juvenile plumage was acquired (SMALL JUV stage). Attainment of flight at 6 to 8 weeks marked the beginning of a second juvenile phase (FLYING JUV stage), which ended with the appearance of first basic plumage at about 4 months (SUBADULT stage). The distances between a foraging adult and its mate ($\Delta$) and between a loafing adult and its mate (□) during the period of territory defense prior to breeding are given for comparison. Sample sizes per point ranged from 9 to 118, with a mode of 32, and standard deviations of raw data were of similar magnitudes as mean values. ANOVA performed on transformed data revealed significant effects of stage and adult behavior, and a significant interaction.

The other species exhibited a similar tendency to avoid foraging near small young. Adult Southern Lapwings continued to forage away from young even after the young were able to fly (Fig. 2).

There was no indication that adults and young foraged in different habitats. Adults and young often foraged in the same locations, but at different times (Fig. 3). In cases in which the young foraged on only a
restricted portion of a territory, adults had used that portion before young were present (Walters, 1980).

The possibility of differential microhabitat requirements was further investigated in Long-toed Lapwings. The habitat was divided into grid units of known vegetation type. For all vegetation types, a grid unit was used less by adults if it was also used by the young than if the young never foraged in it. Furthermore, relationships between vegetation preference and vegetation-specific rates of prey capture attempts were nearly identical in adults and young (Walters, 1980).

These data suggest that avoidance of young by foraging adults was deliberate. Behaviorally it was accomplished by flying or rapidly walking away from young when switching from tending to foraging behavior (see below). The behavior of adults when they did encounter prey in the vicinity of the young may also be revealing. In this situation, adults gave an impression of ambivalence, perhaps between desire to feed and inhibition to feed: strikes at prey were often aborted, and vocalizations indicative of mild alarm were emitted, events that were rarely observed in other foraging contexts.
Showing Food. Only Crowed Plovers showed food to their young. This distinctive behavior involved a unique posture and call that attracted chicks to an adult that had discovered a food source, typically a dung pat containing insect larvae. Once the young arrived and began feeding, the adult moved away. Except for the call, the adult’s behavior was reminiscent of the inhibited foraging exhibited by other species when near young.

Leading, Following, and Gathering Young. These activities were characterized by alert postures and calling that attracted the young. They served to keep chicks near their parents. In leading, adults preceded chicks and often they flew back and forth between the young and a destination, calling, ceasing only when the young finally reached the area. Such episodes were clearly goal-directed, and functioned to move young to new foraging areas. Leading was also employed in short-distance movements.

Adults sometimes maintained proximity with chicks by following them, employing the same calls and postures as when leading. Gathering refers to similar behavior that lacked clear orientation to a goal or a particular chick. The adult moved about, calling, until all the chicks were assembled. Loss of visual contact with chicks and increasing separation between adults and young seemed to trigger this behavior.

3. Benefits of Parental Behaviors to Young

Benefits of parental behaviors to young generally were not documented. I state the following possible benefits as hypotheses, based on the research of others and speculation.

Brooding helps chicks thermoregulate, and is particularly important in shorebirds because thermoregulatory ability develops later in their chicks than in those of other precocial birds (Norton, 1973).

The obvious benefit to young of adult antipredator behavior is that it reduces predation on them. There is some evidence that antipredator behavior is effective: Goransson et al. (1975) found that untended eggs placed near nests of Northern Lapwings (V. vanellus) were less likely to be taken by predators, in this case chiefly gulls, than those placed farther from lapwing nests. Perhaps young also benefit from adults’ monitoring the environment and making decisions about appropriate responses to potential predators for the young, because this enables chicks to concentrate on foraging. Finally, the young may learn to discriminate dangerous predators from other species by observing the responses of their parents.
Interspecific aggression may reduce competition for food experienced by young, and thus enable them to avoid starvation, grow faster, or spend less time foraging and hence exposed to predators (Orians and Willson, 1964; Walters, 1979). Interspecific aggression may also reduce predation on the young if the species lapwings attack attract predators, which may then discover the lapwing chicks (Myers, 1980).

Benefits of vigilance are likely manifested through other parental behaviors: it presumably functions in detecting predators and intruders on the territory, and in monitoring the young.

Foraging away from young may reduce predation on young if moving adults attract predators (Pitelka et al., 1974). This behavior may also reduce competition for food between adults and young, which may benefit young as outlined above.

Showing food to young presumably increases their foraging efficiency. Leading behavior, and perhaps even following and gathering may also increase the foraging efficiency of chicks by guiding them to suitable foraging areas. Leading, following, and gathering behavior also keep chicks in proximity to a tending adult, which may benefit the young in several ways. The probability that a predator will approach a chick closely enough to discover it before being detected by the adults may increase with adult–young distance (Safriel, 1975). So too may the probability that a chick will become lost. Becoming lost is apparently a realistic and fatal possibility in a variety of precocial birds (Ridpath, 1972; Beaver, 1978), including shorebirds (Parmelee et al., 1968; Lenington, 1980).

4. Costs of Parental Behaviors to Adults

Most costs to adults of parental behaviors, like benefits to young, were not documented. However, I did quantify one cost, time adults spent performing parental behaviors. This time could be partitioned into two components: (1) time spent being vigilant and (2) time spent performing other more active parental behaviors (antipredator behavior, interspecific aggression, brooding, showing food, leading, following, and gathering young) (Walters, 1982). The increased time devoted to these activities when young were present was accompanied by a sizable reduction in time spent foraging relative to the nonbreeding (territorial) stage in both Southern Lapwings and Long-toed Lapwings, but not in Blacksmith Plovers (Fig. 4). This reduction in foraging cannot be attributed to seasonal changes in food availability, because the various stages of the breeding cycle were sampled simultaneously in each population. Instead, it suggests that the demands of parenting constrain adults, raising the possibility of energetic stress. In all species, time spent loafing (i.e., preening, rest-
Fig. 4. Percent of time devoted to parental behavior (●) and foraging (★) as a function of the breeding cycle in (A) Long-toed Lapwings, (B) Blacksmith Plovers, (C) Southern Lapwings breeding in pairs, and (D) Southern Lapwings breeding in cooperative trios. The downy and small juvenile stages (defined in Fig. 1) are combined as the unfledged young stage (Unfl), and the flying juvenile and subadult stages are combined as the fledged young stage (Fl). The other stages are incubation (Inc) and the territorial stage (Terr), the period of territory defense prior to breeding and between breeding attempts. Parental behavior is subdivided into active parental behaviors (O), extreme vigilance (alert of Appendix) (□), and moderate vigilance (rest-alert of Appendix) (■). No estimate of moderate vigilance and hence total parental behavior was obtained for the Long-toed Lapwing. Sample sizes are given in parentheses; 95% confidence intervals of the estimates ranged from ± 1% to ± 15%, with most being ± 4–5%. In all four cases, the time budget is not independent of stage of breeding cycle ($\chi^2$, $p < 0.05$). [From Walters (1982).]
ing, or sitting) decreased to an apparent minimum level with the onset of incubation, and thereafter changes in time devoted to parental behavior were directly reflected in foraging time (see Fig. 8).

Antipredator behavior and interspecific aggression probably require considerable energy, but most other parental behaviors probably do not. Therefore, the time required for parental behavior likely is more constraining than the energy required.

There are other possible costs of parental behavior. First, adults risk their lives when attacking predators. Myers (1978) observed the capture and subsequent eating of a Southern Lapwing by a Crested Caracara (*Polyborus plancus*) during an attack by the lapwing upon the caracara (see also Furrer, 1976).

Another possible cost is that avoiding foraging near young may reduce adult foraging efficiency. Also, adult behavior followed a diurnal cycle prior to breeding, but not when young were present. That the diurnal structure of time budgets reverted to the nonbreeding pattern once the young could fly suggests that restructuring activity when young are present is costly to adults. For example, being active at midday, which was characteristic only of adults tending young, might increase costs associated with thermoregulation (Walters, 1980; see also Gibson, 1978).

Finally, vigilance may interfere with other activities, especially foraging. These activities are not compatible because vigilance requires attentiveness toward the young and the surrounding environment, whereas foraging requires attentiveness toward the ground. Therefore, a bird alternating rapidly between these two activities (see below) might be an inefficient forager.

5. Tending Strategies

One striking aspect of parental care in lapwings, besides the behaviors employed, was the coordination between mates. I have described this coordination as a division of labor via two distinct modes of behavior, termed the “off-duty” and “tending” roles (Walters, 1982). An off-duty adult stays away from the young and forages, or occasionally loaf's or is vigilant, whereas the tending adult stays near the young, is vigilant, performs active parental behaviors, or loaf's, depending on the activity of the young, and only rarely forages. This division of labor alleviated the obvious conflict between foraging away from young and tending young.

This coordination between mates may be discerned from patterns in how an adult’s behavior was conditional on the behavior of its mate. Simultaneous responses by mates to important stimuli such as predators and intruders on the territory should make behavior slightly more syn-
Fig. 5. The percent of time that adult Blacksmith Plovers performed the same activity as their mate as a function of the breeding cycle. Expected values (○), observed values (●), and binomial 95% confidence intervals around the latter are presented. The expected value is the sum over the behaviors included in the analysis of the squares of the unconditional probabilities that an adult was in each behavioral state, i.e., the proportion of time spent in that state. The expected value is thus the amount of synchrony expected by chance, i.e., without coordination between mates. If the expected value is significantly different from the observed value (i.e., outside the 95% confidence interval), coordination of activity between mates is indicated. Behavioral states included in the analysis are foraging, loafing (resting, sitting, or preening), alert, away from territory, and other. Similar results were obtained for each of the other species.

chronous than expected by chance in the absence of active coordination between mates. Mates were quite synchronous in their activity when not breeding (Fig. 5, territorial stage), more so than could be accounted for by simultaneous responses to common stimuli. Incubation, of course, introduced an asynchronous coordination between mates as they (both incubate) alternated between incubating and foraging. Mates failed to return to synchronous activity once the eggs hatched; the source of asynchrony during this stage (Fig. 5, downy–flying juvenile) was an alternation between off-duty (foraging) and tending behavior. Both adults sometimes tended simultaneously, but almost never were both foraging away from the young simultaneously. Mates were again synchronous in their activity only when parental behavior waned (Fig. 5, subadult stage).

Spatial relationships provide similar evidence of an alternation of roles. One can compute, based on the proportion of time each adult was within a certain distance of the young, the proportion of time both adults were expected to be within that distance, or beyond that distance, simultaneously if the locations of adults with respect to young were independent of one another. I used 10 or 25 m as the critical distance, depending on how closely young were tended in a particular species. When small young were present, adults were both near or both away less often than expected in all species, but no such pattern was evident once the young were able to fly (e.g., Table I).
Parental Behavior and Clutch Size

Table 1. Percent of Time Both Adults Were Near or Both Were Away from Young in Southern Lapwings

<table>
<thead>
<tr>
<th>Stage</th>
<th>Type value</th>
<th>Both &lt; 10 m</th>
<th>Both &lt; 25 m</th>
<th>Both &gt; 25 m</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Downy</td>
<td>Observed</td>
<td>17&lt;sup&gt;b&lt;/sup&gt;</td>
<td>43&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>248</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>22</td>
<td>49</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Small juv</td>
<td>Observed</td>
<td>5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>38</td>
<td>8</td>
<td>130</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>11</td>
<td>45</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Fledged juv</td>
<td>Observed</td>
<td>5</td>
<td>14</td>
<td>32</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>10</td>
<td>19</td>
<td>32</td>
<td></td>
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</tbody>
</table>

<sup>a</sup> Stages are described in Figs. 1 and 4.
<sup>b</sup> Indicates values significantly different from expected values (binomial test, \( p = 0.05 \)).

Although the species I studied were generally similar in their parental behavior, there were important differences between them, especially in the behavior of the tending (as opposed to off-duty) adult. Southern Lapwings and Crowned Plovers were active tenders: they followed, led, and gathered young constantly, and thus kept near them. In contrast, Blacksmith Plovers and Long-toed Lapwings were inactive tenders: the tending adult was essentially stationary, as it only moved to a new position nearer its young occasionally.

Differences in the tending strategies of these species were manifested in spatial relationships between adults and young, and time devoted to tending behaviors. Distance between nearest (tending) adult and young was greater in inactive tenders than active tenders, and the difference was intensified when young were active, as when foraging (Walters, 1982). Inactive tenders, of course, spent less time performing active parental behaviors, but devoted as much time to vigilance as active tenders. Total time expended on parental behavior was higher in active tenders (Fig. 4).

The Blacksmith Plover differed from all other species in that the tending adult often foraged. The off-duty adult still moved far from the young and foraged, but the adult that remained with the young often foraged too, unlike in Long-toed Lapwings and Southern Lapwings. The tending adult performed some foraging in Crowned Plovers, and this species was unique in showing food to young and in failing to perform interspecific aggression.

These differences between species are mostly quantitative. That is, species differed primarily in the frequency with which various behaviors from a common repertoire were employed. For example, Long-toed Lapwings were inactive tenders, and thus normally did not lead young or call young, but they possessed a call and posture for leading like those
of active tenders, and employed them in exceptional circumstances. Among the parental behaviors exhibited by lapwings, only food-showing was completely absent from the repertoires of some species. Hence, inactive and active tending represent two ends of a continuum rather than a dichotomy.

6. Evolution of Parental Behavior

I now develop an interpretive model of the evolution of parental behavior based on hypothesized effects of several environmental features on the proposed benefits to young of these behaviors. The model is speculative, and is intended as a framework for future research, not a description of results.

Before presenting the model, it is necessary to summarize information about the habitat of each species, emphasizing those aspects included in the model. These are (1) abundance of food, (2) openness of habitat, and (3) abundance of terrestrial predators. Relative abundance of terrestrial predators was estimated from rate of encounters with such species in focal samples. The other two features were not measured. Relative abundance of food was judged from the density of lapwings and other insectivores (which was measured repeatedly) in the habitats of each lapwing species. Relative openness of habitat was judged from my assessment of the amount of obstructing vegetation present (see also Hall, 1959, 1964; Skead, 1955). The model thus considers only very gross differences in habitat features.

Differences between species in these habitat features and in parental behavior are summarized in Table II. Crowned Plovers inhabited dry, open plains far from water. This was the most open habitat, and it contained few terrestrial predators and sparse food. Blacksmith Plovers inhabited open areas of various kinds adjacent to water. This habitat was nearly as open as that of Crowned Plovers, and contained more food and more terrestrial predators. Southern Lapwings occupied a habitat in Venezuela roughly equivalent to that of Blacksmith Plovers in Kenya. However, Southern Lapwing habitat was not as open as that of Blacksmith Plovers (but see below). Long-toed Lapwings inhabited surface vegetation within marshes, an unusual, distinct habitat that was open, rich in food, and of course devoid of terrestrial predators.

Active ness of Tending. The model focuses on adult—young distance because of the hypothetical influence of this variable on the effectiveness of antipredator behavior and the probability of young becoming lost (see above). Adults control adult—young distance through activeness of tending: the more actively they tend, the smaller the average (tending) adult—
Table II. Features of Parental Behavior and Ecology of Lapwing Species

<table>
<thead>
<tr>
<th>Lapwing species</th>
<th>Parental behaviors</th>
<th>Environmental factors</th>
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<tbody>
<tr>
<td></td>
<td>Showing food</td>
<td>Active tending</td>
</tr>
<tr>
<td>Long-toed</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Blacksmith</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Southern</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Crowned</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

*a Parental behavior and environmental factors are described in text. For parental behaviors, a + indicates that the behavior is present in the species, a - that it is absent. For environmental factors, the development of a factor is rated as +, 0, or - for each species, + indicating highest development, - lowest development, and 0 intermediate.*
Fig. 6. Model of the evolution of lapwing parental behavior. Parental behaviors are outlined by broken lines, environmental factors by solid lines. A (+) denotes a direct relationship between two variables, a (−) an inverse relationship. For example, A → B indicates that an increase in A causes an increase in B, whereas A → B indicates that an increase in A causes a decrease in B.
young distance (Fig. 6). Several ecological factors are expected to increase adult–young distance, independent of adult behavior. Chief among these factors is sparse food, because it increases mobility of young by forcing them to forage over broader areas. These factors are expected to lead to more active tending, because this is the adults' means to balance environmental effects on adult–young distance. If two species exhibit similar adult–young distances, that with the sparsest food supply must tend more actively to maintain it.

Other ecological factors may reduce the need to stay near young, and hence allow adults to tend less actively. These factors include high visibility (openness of habitat) and low density of terrestrial predators. Aerial predators are not considered because they were detected at such great distances that a small change in adult–young distance likely has a much smaller effect on exposure to these predators than to terrestrial predators (Walters, 1980). The balance here is on probability of becoming lost and efficiency of antipredator behavior (Fig. 6). Parents can allow their young to stray without risk of predation if there are few terrestrial predators or if high visibility allows them to detect predators at great distances. Also, parents can more easily monitor straying chicks in open habitats, and hence can prevent them from becoming lost without staying as near to them.

This model can account for differences in activeness of tending among the species studied. The Long-toed Lapwing differed from the Southern Lapwing in being an inactive, rather than active, tender. There were four differences between these two species that might affect activeness of tending (Table II). (1) Long-toed Lapwings were not vulnerable to terrestrial predators, but Southern Lapwings were. (2) Long-toed Lapwing habitat was more open than Southern Lapwing Habitat (but see below). The ability of Southern Lapwings to occupy more closed habitat may be attributed to their reliance on probing in the substrate when foraging (Fig. 6). Other species relied more on the pecking methods characteristic of charadrids, which are ineffective in tall or dense vegetation (Klomp, 1954; Burton, 1974). (3) Young Long-toed Lapwings were less mobile than young Southern Lapwings owing to a richer food supply and a less negotiable habitat. (4) Long-toed Lapwing territories were much smaller than those of Southern Lapwings, again presumably due to their richer food supply (Walters, 1980). All of these factors reduce the need for active tending in Long-toed Lapwings compared to Southern Lapwings.

Active tending in Crowned Plovers is attributed to the great mobility of their young, necessitated by a sparse food supply. Inactive tending in Blacksmith Plovers is attributed to their open habitat. This influence must be strong enough to outweigh the effects of high predator density and
having young of intermediate mobility, both of which select for active tending.

Other Parental Behaviors. In addition to activeness of tending, the model also treats (1) interspecific aggression, (2) showing food, (3) foraging away from young, and (4) foraging while tending (Fig. 6). Interspecific aggression is hypothesized to benefit chicks by reducing the number of other birds in their vicinity, because intruders either compete with young or attract predators (see above). If young are highly mobile, the benefits of defending the area around them may be greatly reduced. In the case of defending against competitors, reducing the density of intruders in the area surrounding the young will alter the amount of food removed by competitors from a particular location only during the brief period the young are there. The intruders could forage there prior to and subsequent to the chicks' passing through. Unless resources renewed very rapidly, aggression would provide little increase in availability of food.

Benefits derived from defending against birds that might attract predators may also be reduced by mobility of young, depending on the distance and time interval over which the relevant predators respond to prey density. If predators react to changes in prey density over periods of days or hours, or over great distances, defending the area around the chicks will have little effect on attraction of predators by intruders. Victims of aggression, by fleeing only a short distance, would remain sufficiently near the young that they might still attract predators to them.

The model therefore asserts that the presence of mobile young selects against interspecific aggression (Fig. 6). This accounts for the lack of interspecific aggression in the species with the most mobile young, Crowned Plovers (Table II).

The benefits of parents foraging away from young are the same as those of interspecific aggression (see above), and therefore the former should be affected by mobility of young in the same way as the latter (Fig. 6). This accounts for foraging by tending adults in Crowned Plovers. Blacksmith Plovers foraged near young to an even greater degree. The model attributes this to the combination of fairly mobile young and large tending adult–young distances resulting from inactive tending (Table II). Both should reduce the effect of foraging by tending adults on competition between adults and young, and possibly that on attraction of predators by adults.

The model relates showing food directly to food abundance (Fig. 6). The species with the sparsest food supply (Crowned Plover), and hence the greatest need to improve the foraging efficiency of its young, is the only one that exhibited food-showing.
B. Parental Behaviors of Other Shorebirds

1. Types of Behavior

Quantitative data on parental behavior comparable to these lapwing data have not been collected for other shorebirds. There are, however, numerous qualitative descriptions of parental behavior, plus a few quantitative time budget studies from which information about parental behavior can be inferred. These data are not sufficient to evaluate the model of the evolution of parental behaviors presented above, but they enable a general description of shorebird behavior and a limited review of tending strategies.

The parental behaviors of lapwings described above typify those of shorebirds in general. Brooding, vigilance, and crouching by the young in response to adult alarm calls are apparently universal. Leading seems to occur in all species except those few whose young are nidicolous (Table III). It is most often employed in moving chicks from a nesting area to a foraging area after hatching (Miller, 1979a). A rare behavior with perhaps the same function as leading is carrying of young, which occurs in woodcocks (Scolopax sp.) (Ingram, 1978) and jacanas (Jacanidae) (Hopcraft, 1968). In both groups the behavior has evolved in a context in which leading young is a difficult means of moving them, either because of the distances covered (woodcocks) or the difficulty in negotiating the substrate (jacanas).

Feeding of young is common among shorebirds, but is closely correlated with taxonomy. All members of some families feed young (Rosratulidae, Dromadidae, Haematopodidae, Burhinidae, Glareolidae, Chionididae, Pluvianellidae), whereas no members of the remaining families do (Jacanidae, Ibidorhynchidae, Charadriidae, Recurvirostridae, Thinocoridae) with the exception of the Scolopacidae. Feeding of young is typically associated with unusual foraging morphology (Rosratulidae, Glareolidae) or behavior (Haematopodidae, Burhinidae, Dromadidae, Pluvianellidae). Perhaps developmental constraints on the acquisition of such foraging modes lead to feeding of young. However, the Cursoriinae do not have unusual foraging but feed young, and a number of species with seemingly equally difficult foraging requirements do not feed young (Ibidorhynchidae, Recurvirostridae). Of course, young may feed on different prey than adults in exceptional species, and feeding of young may thus correspond closely with ecology. However, in the absence of data on the foraging of shorebird chicks, an important phylogenetic component in the evolution of feeding of young remains a viable possibility.
Table III. Parental Behaviors of Shorebirds

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Feed young</th>
<th>Forage away from young</th>
<th>Alternate tending</th>
<th>Lead young</th>
<th>Interspecific aggression</th>
<th>Distract predator</th>
<th>Attack predator</th>
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<td>Thinocoridae</td>
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* Notation as follows: ++ indicates the behavior occurs commonly within the taxa; + indicates that it occurs but infrequently; - indicates that it does not occur.

* Young are nidicolous; these behaviors are therefore precluded.

* Only one parent tends brood, so this behavior is not possible.
Although some scolopacids feed young (Table III), feeding is more limited than in other taxa that feed young. Most of these scolopacids provide their young with only a little food, and only during the first few days after hatching (e.g., Ruthke, 1977). Feeding is most regular and most substantial in snipes and woodcocks, but even in these species the young procure much of their own food initially and all of it once they are older. The scolopacids may therefore be generally classified as a taxon in which young feed themselves.

It is difficult to evaluate the prevalence of foraging away from young and alternating tending and off-duty roles among shorebirds that do not feed young due to lack of appropriate data. Explicit suggestions of such behavior have been reported for a variety of species in which both adults care for young, and these are the basis for the analysis in Table III. Such behavior may be widespread.

In species in which only one adult cares for young, the second adult may be considered to engage in the off-duty away role permanently. In some of these species, the second adult simply deserts the family, but in others it is active in the off-duty role. That is, it joins in antipredator behavior, is vigilant, joins in interspecific aggression, and may even rarely relieve its mate and tend the young. Such behavior has been reported in jacanas (Jenni and Betts, 1978), polygynous lapwings (Laven, 1941), plovers (Phillips, 1980), godwits (Hagar, 1966), phalaropes (Hildén and Vuolanto, 1972), and seedsnipes (Maclean, 1969).

Predator-directed antipredator behaviors are characteristic of shorebirds (Table III), but the particular behaviors employed, and the relative frequency with which each is employed, vary considerably among species (see Gochfeld, this volume). Larger species employ aggressive responses more frequently and to a wider range of predators than smaller species (Sordahl, 1981). However, even small shorebirds react aggressively to certain predators, especially avian ones that are relatively small and pose little threat to adults, such as crows and gulls. Aggression ranges from close swooping to circling above the predator to threats delivered from the ground.

These aggressive behaviors merge into distraction behaviors. For example, calidridine sandpipers sometimes hover in the face of a human passing near their nest or young (Brown, 1962). Behaviors that are more clearly distracting include loud calling and a variety of elaborate stereotyped displays, specifically false-incubation, crouched running, injury-fearing, and the rodent-run, a bizarre display in which the bird runs away with tail spread emitting a squealing vocalization. Which displays are used varies among species. Smaller shorebirds rely more on distraction (as
opposed to aggression) than do larger ones, but even the largest, boldest shorebirds employ distraction regularly.

Interspecific aggression is also widespread, but its prevalence is somewhat unclear due to lack of sufficient study (Table III). Even less is known about some of the other parental behaviors observed in lapwings, precluding their inclusion in Table III. Following and gathering have not been explicitly described as defined above for other shorebirds. Hints of sophisticated discrimination of predators exist for other species, e.g., Sociable Plover *V. gregarius* (Meinertzhagan, 1954; Bannerman, 1961), but documentation is nonexistent for shorebirds, and is rare for birds in general (but see Mueller, 1976; Grubb, 1977; Ficken and Witkin, 1977). Similarly, showing food has only been documented for Crowned Plovers, but there are hints of such behavior in other species, notably calidridines (Parmelee, 1970; Fjeldså, 1977).

2. Tending Strategies

Species for which the data are sufficient to evaluate tending strategies and time costs of tending are very few. Lenington (1973, 1980) provides a clear description of inactive tending in Killdeer (*Charadrius vociferus*). Semipalmated Sandpipers (*Calidris pusilla*) are fairly active tenders immediately after hatching, but then become inactive judging from the descriptions of Ashkenazie and Safriel (1979a,b). Time budget data indicate that foraging is reduced during the period of active tending, but time devoted to parental behavior cannot be determined because, as in most such studies, the behaviors comprising the ethogram do not correspond to parental behaviors. That is, a category may include some behavior that is parental and some that is not. This is especially problematic in determining time devoted to vigilant behavior.

The most complete time budget data, and least problematic in this respect, are those provided by Maxson and Oring (1980) for the Spotted Sandpiper (*Actitis macularia*) and Gibson (1978) for the American Avocet (*Recurvirostra americana*). Because both species are inactive tenders, the time cost of caring for young lies primarily in time devoted to vigilant behavior (Fig. 7). Time devoted to parental behavior is detracted mostly from loafing and maintenance activities (preening, bathing), so that foraging is reduced little or not at all when young are present, as in Blacksmith Plovers (compare Figs. 4 and 7). Tending young apparently constrains time budgets less in these species than in Crowned Plovers, Long-toed Lapwings, or Southern Lapwings.
C. Discussion

Study of the parental behavior of shorebirds has barely begun. There is a need for better descriptions of parental behavior, especially with respect to subtleties such as activeness of tending, alternation of tending duties, and predator-discrimination abilities. This area of shorebird biology must then progress beyond the descriptive stage through documentation and quantification of benefits to young and costs to adults of parental behaviors. Specific hypotheses about the evolution of behavior may then be tested. The ideas presented here about costs and benefits and about the evolution of parental behavior are speculative, but provide a heuristic framework for such future research.

The proposed model of the evolution of parental behaviors can easily be tested by comparisons between species. It may also be tested by comparisons of populations of a single species. For example, Blacksmith Plovers breed in some habitats that are much more closed than that of the study population (Walters, 1980); the model predicts they will tend more actively in those habitats. This prediction was verified for Southern Lapwings. Two of the seven successful breeding pairs observed inhabited a field that was much more open than the shrubby areas inhabited by the remaining birds. The mean tending adult–young distance was substantially greater in these two pairs than in any of the other five, presumably because adults tended less actively in the more open area (Walters, 1980).
Although the data are few, it is already clear that parental behavior cannot be regarded as a trivial activity in shorebirds. It imposes considerable demands on adults in some species, but does not in others. Having shown that the usual assumptions about parental behavior in shorebirds are unreasonable, it is necessary to reevaluate the effects of parental behavior on other aspects of shorebird life-history, such as clutch size and mating systems. Time costs of parental behavior and their variation among species have considerable consequences for single-parent care, and thus may affect the evolution of shorebird mating systems (Walters, 1982). The relationship between costs and benefits of parental behavior and brood size has similar implications for the evolution of clutch size (see below). Studies of shorebird parental behavior may therefore be of more general importance than has been previously realized.

III. CLUTCH SIZE

The clutch sizes of shorebirds are described by Maclean (1972b). More recent information has increased the accuracy of our estimates of clutch size for a few species, but these alterations are so few that a new review is unwarranted. Instead, I shall examine the evolution of clutch sizes in shorebirds, using as a basis the data provided by Maclean (1972b) and additional information summarized by Johnsgard (1981).

Variation in shorebird clutch sizes follows a unique pattern. The most striking aspect is a sharp truncation at the maximum clutch size of four. Four is the most common modal clutch size, but no species lays more than four eggs. Many species lay fewer, however. Clutch size theory must therefore answer two questions to explain shorebird clutch sizes: (1) why no species lays more than four eggs and (2) why many species lay clutches that are reduced in size relative to the most common clutch size of four.

Lack’s work (1947, 1948, 1954, 1968) laid the foundations of current theories about the evolution of clutch size in birds. He postulated that ability to feed young is the factor that limits clutch size in most birds, and that ability to form eggs is the limiting factor in species that do not feed young. Lack’s basic premise was that the number of eggs laid corresponds to the maximum number of offspring that can be raised, which is determined by the proposed limiting factors. This premise has subsequently been qualified to read that the number of eggs laid corresponds to the maximum number of offspring that can be raised with the reproductive effort appropriate for a single clutch (i.e., optimal working capacity; Royama, 1966). That is, individuals maximize their reproductive
success over lifetimes, not within a single clutch, and adjust effort in any one year accordingly (Williams, 1966; Charnov and Krebs, 1974; Goodman, 1974). Many birds thus lay a smaller clutch than that which produces the most young with maximum reproductive effort (von Haartman, 1971; Perrins and Moss, 1975; Drent and Daan, 1980).

This does not alter the core of Lack's theory, however. There may still be a single reproductive activity that limits clutch size by reaching the optimal working capacity of adults. The best candidates for this activity are still those proposed by Lack, namely feeding of young for most species and ability to form eggs for species that do not feed young. Clutch size is then determined by the match between the food required for these activities and the food obtained by adults foraging at optimal working capacity.

Clutch size thus varies both between and within species in correspondence with not only limiting factors, but also with differences in how reproductive effort is apportioned, because this affects optimal working capacity (Cody, 1966; Murphy, 1968; Foster, 1974a; Payne, 1974; Brockelman, 1975; Stearns, 1976, 1977; Howe, 1978), and with availability of food during breeding, because this affects production per reproductive effort (Ashmole, 1963; Royama, 1969; Ricklefs, 1970, 1980; Foster, 1974b; Slagsvold, 1975; Owen, 1977).

A. Species That Feed Young

To begin, I divide shorebirds into species that feed their young and those that do not, for the proposed mechanisms of clutch size limitation differ depending on whether or not young are fed.

Species that feed their young generally have clutch sizes less than four (Maclean, 1972b) (Table IV). (The issue of truncation at a clutch size of four is hence moot for this subgroup of shorebirds.) That feeding young leads to reduced clutch sizes can only be tentatively concluded, however, because species that feed young are generally found in geographic regions (tropical, southern) where clutch sizes tend to be reduced even if young are not fed (see below). Furthermore, whether or not young are fed varies only between families, not within, and there are differences at the family level in tendency toward reduction of clutch size among species that do not feed young (see below). One might therefore attribute reduction of clutch sizes in species that feed young to the same factors that cause geographic and taxonomic differences among species that do not feed young (see below), and postulate that clutches are limited by the same factor in both. However, the association between reduction of clutch size
and feeding young is so strong (compare Tables IV and V) that the most parsimonious hypothesis is that feeding of young, not geography or taxonomy, is the key factor. It follows that the factor limiting clutch sizes differs between species that do not feed young and those that do, and feeding of young is implicated in the latter case. According to this hy-

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thesis, clutch sizes may be viewed as a match between optimal working capacity, determined by the life-history strategy, and the amount of food provided young per unit of feeding effort, determined by food availability.

There is no evidence that shorebirds are limited in their ability to feed young comparable to that which exists for many altricial birds (e.g., Crossner, 1977). There is also no evidence to the contrary, nor of any other limiting factor. Lack's original hypothesis therefore still stands, but by default rather than due to additional empirical support. Research is needed to distinguish between it and other viable limiting factors, such as all those proposed for species that do not feed young (see below).

B. Species That Do Not Feed Young

The majority of shorebirds do not feed their young. Variation in the clutch sizes of these species may be summarized as follows (Table V).

1. A sharp truncation at the maximum clutch size of four, with over 70% of the species having a modal clutch size of four.
2. A strong tendency toward the maximum clutch size in northern regions, but an approximately equal division between maximum and reduced clutch sizes in tropical and southern regions.
3. A tendency for some taxa (Jacanidae, Vanellinae, Recurvirostridae) to have larger clutches than other taxa (Charadriinae) independent of the effect of geography.

I shall now examine factors proposed to limit the clutch sizes of shorebirds that do not feed their young and determine their adequacy in accounting for these patterns. These are (1) egg-formation ability, (2) incubation ability, (3) nest predation, (4) phylogenetic inertia, (5) and parental behavior.

1. Egg-Formation Ability

I begin with the explanation proposed by Lack, that clutch sizes are limited by the ability of females to form eggs. The critical element in egg-formation ability has not been identified for shorebirds. Most versions seem to assume it is energy, although it could also be some specific nutrient.

The egg-formation hypothesis is less attractive for shorebirds than for other precocial birds that do not feed young because the former lay much smaller clutches than the latter. However, shorebirds produce unusually large eggs (Rahn et al., 1975) so that their clutch weights are in
fact not unusually small among precocial birds of comparable body weights. Anatids have much greater clutch weights than shorebirds at comparable body weights (see data in Lack, 1968), but clutch weights of phasianids average only half those of anatids (Rahn et al., 1975), which is even less than those of shorebirds. Shorebirds therefore are not atypical among precocial species in reproductive output. However, they may be atypical in reproductive strategy, investing heavily in each egg at the expense of producing a larger number of eggs. In other birds, egg size is positively correlated with viability of young (Schifferli, 1973; Nisbet, 1978; Al-Murrani, 1978), and shorebird species that are unusual in regularly laying two or more clutches rapidly also have unusually small eggs (Howe, 1975; Osborne and Bourne, 1977; Ross, 1979). General differences between shorebirds and other precocial birds in clutch size may thus reflect a difference in life-history strategy rather than in mechanism of clutch size limitation.

Evidence directly supporting the egg-formation hypothesis is non-existent for shorebirds, however. That clutch weights in smaller shorebirds often exceed female body weight (Rahn et al., 1975) intuitively reinforces the notion that females have a limited capacity to produce eggs, but this in no way constitutes evidence supporting the hypothesis. There are data indicating that the food supply affects the timing of egg laying (but not clutch size) in Northern Lapwings (Högstedt, 1974), but as in all such experiments, it is not clear whether the effects of food supplements are manifestations of the ultimate or proximate determination of clutch size (Drent and Daan, 1980). Confusion about levels of explanation is a serious problem in clutch size research generally.

Not only are data supporting the hypothesis lacking, but contradictory evidence exists also. Most striking are the results of egg removal experiments with Northern Lapwings. Females of this species normally lay four eggs, but can be induced to lay one or two additional eggs by removing the initial eggs of a clutch as soon as they are laid (Rinkel, 1940; Klomp, 1951). These experiments suggest that clutch size is proximately regulated by feedback from the first egg laid as it is in gulls. Gulls respond to removal of eggs in exactly the same manner as Northern Lapwings, and may be induced to lay up to eight eggs in addition to the usual four. Apparently, stimuli from incubating the first egg halt follicle production, thus determining clutch size (Paludan, 1952; Weidmann, 1956; Parsons, 1976). If these stimuli are removed, eggs continue to be produced until the bird decides to abandon the nest.

One does not expect such a proximate means of limiting clutch size if ability to form eggs is the ultimate limiting factor. Instead, one expects the proximate mechanism to be related to the condition of the female, as
Fig. 8. Percent of time spent foraging (F) and loafing (L; resting, sitting, or preening) as a function of the breeding cycle in (A) Southern Lapwings and (B) Blacksmith Plovers. Stages of the breeding cycle are as defined in Figs. 1 and 4 except that the mating stage is added. This stage lasts from the initiation of nest building until the start of incubation and is the period during which eggs are formed. Time budget is not independent of stage of breeding cycle in either species. Sample sizes per stage range from 43 to 462, with a mode of 158.

It is in Arctic-nesting geese (Klomp, 1970), the only group of nidifugous birds for which there is conclusive evidence that ability to form eggs limits clutch size (Ryder, 1970; Inglis, 1977; Ankney and MacInnes, 1978; Ankney, 1979; Raveling, 1979). In geese, levels of protein reserves appear to proximately control clutch size (Ankney and MacInnes, 1978; Raveling, 1979).

The difference between geese and shorebirds in proximate regulation of clutch size intimates a difference in ultimate regulation. Further evidence contradicting the egg-formation hypothesis comes from lapwing time budget data. If females are limited by their ability to obtain food, foraging time should be at a premium during egg formation (unless foraging profitability varies radically as a function of time). An indication of this would be that loafing is kept to a minimum at this time. Instead, loafing was as frequent during egg laying as during other stages of the breeding cycle, sometimes more frequent (Fig. 8). Decreases in loafing were observed during other periods thought to be demanding, for example when small young were present in Southern Lapwings (Fig. 8A). The limited data collected from birds of known sex indicated that these conclusions held for females specifically as well as adults generally. Time budgets of other shorebirds give similar results (Gibson, 1978; Ashkenazie and Safriel, 1979b; Maxson and Oring, 1980) (Fig. 7). There are no indications
that foraging time is at a premium when eggs are being formed in shorebirds.

It is difficult to account for truncation at the maximum clutch size with the egg-formation hypothesis. This requires that differences between species in food availability, life-history strategies, and egg size always balance one another so that the amount of food females are able to procure is sufficient to produce only four eggs, no more. No such truncation exists in any other group of nidifugous birds.

The egg-formation hypothesis can account for reduced clutches only to the extent that species with reduced clutches are less efficient at converting a given amount of available food into eggs. However, one does not expect to account for all variation in egg number by the factor limiting clutch size. This factor will surely account for some of the variation, but its influence must be separated from the suite of other influences on clutch size. In the case of the egg-formation hypothesis, life-history considerations determine the foraging effort, food availability affects the returns on this effort, and ability to convert this food into eggs then determines egg number. Differences between taxa in tendency toward reduced clutch sizes may therefore reflect, at least in part, differences in life-history strategies or food availability related to ecological dissimilarities between these taxa. Similarly, greater tendency toward reduced clutches in southern regions (which house mostly maritime species) and tropical regions compared to northern regions may be due to greater seasonality, and therefore food available per individual, in the latter (Ashmole, 1963; Ricklefs, 1980). There may also be regional differences in life-history attributes if, for example, competition or predation is generally more intense in southern coastal regions and the tropics than in the Arctic regions where most northern shorebirds breed. Until the influences of life-history variables and food availability can be measured, it will be difficult to judge the egg-formation hypothesis on its ability to account for reduced clutch sizes.

In summary, the traditional explanation that food available to the laying female limits shorebird clutch sizes is not well supported by the limited data available. In the absence of more complete data, it remains a viable hypothesis, but the need for alternatives is compelling, and several have been suggested. I shall now review these, and offer yet another.

2. Incubation Ability

The possibility that shorebird clutch sizes are limited by the ability of adults to incubate eggs has received considerable attention recently. Miller (1979b) has proposed that truncation at the maximum clutch size
is due to the need to conserve heat during incubation. Due to the shape of shorebird eggs, four eggs can be aligned such that heat lost when the clutch is uncovered is less than that for any possible arrangement of a larger or smaller number of eggs. This hypothesis addresses only the issue of truncation at the maximum; another limiting factor must be postulated where clutch sizes are reduced. Andersson (1978) offers the more general hypothesis that brood patch area limits incubation ability and thus clutch size.

Hills (1980) provides experimental evidence of limitation by incubation ability. Her adding an egg to four-egg clutches resulted in a dramatic decline in hatching success in six species. Similarly, Gibson (1971) reports that American Avocets have difficulty incubating abnormally large clutches that occur naturally. It is not clear which, if either, of the proposed mechanisms accounts for these effects.

Despite these intriguing results, the incubation-ability hypotheses have some serious drawbacks. Most birds have no difficulty incubating abnormally large clutches (e.g., Frederickson, 1969). Some claim that many shorebirds also can incubate abnormally large clutches successfully, although this needs to be documented more conclusively (Shipley, 1980). Also, some species with unusual mating systems may routinely incubate more than four eggs under natural conditions (Walters and Walters, 1980). More importantly, Andersson’s hypothesis begs the question of adaptation, i.e., it offers no explanation of variation in brood patch area. Miller’s hypothesis does not thus suffer, but has a limited application, as noted above.

Another interpretation of incubation effects is that they reflect secondary adaptations. That is, egg shape may be a secondary adaptation evolved in the context of a clutch size, four, determined by other causes, rather than the factor ultimately limiting clutch size. Similarly, brood patch area may evolve to match the normal clutch size, which is determined by other factors (Klomp, 1970). Andersson (1976) proposes that brood patch number in Jaegers (Stercorarius longicaudus) is such a secondary adaptation, and it prevents these birds from successfully incubating experimentally enlarged clutches.

If egg shape and brood patch area are secondary adaptations, they should be evolutionarily malleable, and should change when it becomes otherwise advantageous to have a different clutch size. If these features are instead ultimately limiting clutch size, it should be demonstrable that other hypothesized factors are not limiting. For example, it should be possible to show that shorebirds can form more than four eggs and raise more than four young, but the thermal benefits due to egg shape outweigh the advantages of producing additional offspring.
In conclusion the incubation-ability hypotheses have several theoretical problems, but are better supported by evidence than most alternatives, and certainly are viable.

3. Predation on Nests

It has been suggested that a small clutch may be an adaptation to high nest predation (Oiring and Knudson, 1972; Perrins, 1977). Females lay at best one egg per day, so the length of time a nest is exposed to predation increases with clutch size. Because most predators tend to consume entire clutches, a small clutch may on the average produce more young than a larger one due to a difference in the proportion of clutches lost to predators. However, calculations by Perrins (1977) clearly show that shorebird clutch sizes are too small for decreased nest predation to outweigh the advantages of increasing the number of young under realistic predation rates. No other mechanism by which clutch size could be limited by predation has been offered. Predation pressure may of course be one of the factors determining life-history strategy (i.e., apportionment of reproductive effort), but this role should be distinguished from its possible role as a limiting factor. Currently there is no viable predation hypothesis with respect to the latter role.

4. Phylogenetic Inertia

Maclean (1972b) relates shorebird clutch sizes to historical factors, hypothesizing that species have maximum clutch sizes of four in the area in which their taxa originated and reduced clutches in other regions subsequently invaded. He thus relates reduction in clutch size to unknown ecological changes accompanying invasion of new areas, and identifies the maximum of four as the ancestral clutch size. He offers no explanation of the evolution of the ancestral clutch size.

One might allow history an even greater role, although Maclean (1972b) does not do so, and propose that present clutch sizes are not adaptive, but are historical remnants. That is, they result from phylogenetic inertia (Wilson, 1975, p. 32), the heritable variability necessary for a different clutch size to evolve being absent. Known variability is too great for this to be a reasonable general hypothesis, but it may apply to the issue of truncation at maximum clutch size. Clutches of more than four eggs have been reported for many species (Johnsgard, 1981), but some such clutches are known to result from two females laying in a single nest either by egg dumping (Gibson, 1971) or cooperative breeding (Walters and Walters, 1980). Claims that five-egg clutches are laid by a single
female (e.g., Bannerman, 1961, p. 97) need to be verified to demonstrate that the variability necessary for a clutch size greater than four to evolve exists, and this variation must be shown to be heritable.

This is the only way in which the phylogenetic inertia hypothesis can be falsified. That four was historically the optimal clutch size cannot be tested. Other hypotheses can be more easily falsified, and this (if I may be permitted an opinion based on discussions with colleagues) seems the primary source of strength for the phylogenetic inertia hypothesis. It is a default option, to which one turns when confronted with the difficulties with the other hypotheses. It has no empirical basis in its own right, and is unlikely to gain one.

5. Parental Behavior

Parental behavior has received little attention as a factor limiting clutch size in shorebirds that do not feed their young because it was assumed that parental behavior is not demanding in such species. This assumption is actually irrelevant (see below), and may be unreasonable in addition (see above). It may therefore be worthwhile to reconsider that some form of parental behavior limits the clutch sizes of shorebirds that do not feed their young.

Safriel and Shipley Models. For parental behavior to limit clutch size, the costs and/or benefits of parental behavior must be sensitive to brood size, regardless of how demanding parental care is. The relationship between costs and/or benefits and brood size is a necessary condition for such a mechanism, whereas a large cost and/or benefit is neither necessary nor sufficient.

Safriel (1975) suggests a mechanism for a relationship between brood size and benefits of parental behavior. He proposes that young must disperse in order to forage effectively, that brood dispersion therefore increases with brood size, and that the distance between adult and young increases with brood dispersion (and thus brood size). Once broods exceed a certain size, chicks are too far from adults to be protected adequately, increasing the likelihood of predation. He conjectures that predators are able to take all or most of a brood once they detect a chick, so that reproductive success decreases as brood size increases above the level at which adults can adequately protect their young. Safriel found that artificially enlarged broods of Semipalmated Sandpipers were more likely to disappear than normal broods, as predicted by the hypothesis, assuming predation is the cause of disappearance.

Shipley (1980) presents an alternative model. He also assumes that the ability of adults to protect their young from predators is a function
of the dispersion of young, and that dispersion is a function of brood size. He proposes that for geometric reasons, four is the optimal number for minimizing adult–young distance and overlap in chick foraging areas simultaneously. If a fifth chick is added to the brood, either adult–young distance or overlap in chick foraging areas must be greatly increased. Shipley offers no evidence that shorebird broods actually assume the geometric configurations he imagines.

Both models are primarily concerned with explaining truncation at the maximum shorebird clutch size. However, the relationship between predation and foraging efficiency hypothesized can easily be imagined to limit clutch sizes to a reduced number under certain conditions, namely those of extreme predation pressure or foraging dispersion.

**Lapwing Model.** Although Safriel’s (1975) pioneering study provides indirect evidence that parental behavior limits clutch size, the basic assumptions of the above models are speculative. I collected data from lapwings to test these assumptions. The results, described in more detail elsewhere (Walters, 1982), confirmed the assumptions only in part, leading me to propose a more general model describing how parental behavior might limit clutch size in shorebirds. I shall now summarize these results and the model based on them.

The models of Safriel (1975) and Shipley (1980) assume that parent–young distance increases with brood size. This may be true of inactive tenders, but not of active tenders (Table VI). In the actively tending Southern Lapwing, the tending adult stayed as near each chick in a brood of two as it did a single chick. Addition of a third chick did not appear to alter tending adult–young distance either, but the data were insufficient to test this adequately (Walters, 1980). There was no significant increase in tending adult–young distance with increased brood size in inactive
Table VII. Effect of Brood Size on Time Budgets of Adult Southern Lapwings

<table>
<thead>
<tr>
<th>Stage of breeding cyclea</th>
<th>Brood sizeb</th>
<th>Behavioral state</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Foragec</td>
<td>Parental behavior</td>
</tr>
<tr>
<td>Downy</td>
<td>1</td>
<td>27</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>2 or 3</td>
<td>19</td>
<td>59</td>
</tr>
<tr>
<td>Small</td>
<td>1</td>
<td>24</td>
<td>48</td>
</tr>
<tr>
<td>juvenile</td>
<td>2 or 3</td>
<td>15</td>
<td>66</td>
</tr>
</tbody>
</table>

a Stages are described in Fig. 1.
b Time budget is statistically independent of brood size in the downy stage, but not the small juvenile stage $\chi^2, p = 0.05$.
c Values are given as percentages of total time, although statistical analyses were performed on raw frequencies.

tenders either. However, sample sizes were inadequate, and a strong trend toward a positive correlation was evident for both species of inactive tender examined (Table VI). Therefore, that distance increases with brood size in inactive tenders remains a reasonable assumption. Indeed, a brood size effect seems inevitable considering that inactive tenders rarely directed distance-reducing behaviors such as following at young, or gathered broods (see above), and that chicks showed no tendency to group when foraging (Walters, 1980).

The mechanisms for limiting clutch size proposed by Safriel and Shipley are therefore inappropriate for active tenders, and another must be offered. Although Southern Lapwings stayed as near each chick in a large brood as a small one, time budget data suggest that they had to work harder to do so. That is, the amount of time devoted to parental behavior increased with brood size, and time devoted to foraging decreased (Table VII). This suggests a means by which parental behavior might limit clutch size in active tenders: as brood size increases, the demands of parenting increase until the optimal working capacity of adults is reached, which point marks the optimum brood (clutch) size.

The few data on clutch size collected from the study populations suggest that active tenders have reduced clutch sizes, whereas inactive tenders do not (Walters; 1982). The lapwing model of limitation of clutch size by parental behavior therefore incorporates active tending as a factor in reducing clutch sizes, due to the time demands of parental behavior. This clutch size model is thus linked to the model of the evolution of parental behavior presented above (Fig. 6). Those factors that are hypothesized to select for active tending (low visibility, high predation,
sparse food) lead to reduced clutch sizes. Conditions that lead to inactive tending favor the maximum clutch size of four.

The lapwing model assumes that adult–young distance is positively correlated with chick mortality, as do those of Shipley and Safriel. The evolution of active tending depends on this relationship (see above), and the model also contends that it is this relationship that limits clutch size to four in inactive tenders. That is, the reduction in benefits of tending as adult–young distance increases with brood size outweighs the advantage of producing additional young above a brood size of four. For this mechanism to be viable, these reductions must be very sharp between broods of five and four.

Safriel’s (1975) model may thus be subsumed within mine as the explanation for inactive tenders, if one adds prevention of becoming lost to prevention of predation as a benefit of small adult–young distance, and his experimental results are in accordance with the model if Semipalmated Sandpipers are indeed inactive tenders (see above). The model also includes a second mechanism for active tenders, limitation of clutch size by time available for caring for young, which leads to reduced clutch sizes. Clutch size is then linked to environmental conditions through factors that determine activeness of tending.

In conclusion, the parental behavior hypothesis is also viable. Having received relatively little attention, fewer objections have been raised to it than to other hypotheses, but it also has less supporting evidence than most others.

C. Discussion

The data base for clutch size research is good, although it could be improved by better documentation of differences between populations within species. There is also ample development of theory designed to explain clutch sizes. What is now required is the testing of explicit hypotheses concerning the evolution of clutch size in shorebirds.

To conduct such research, effects of food availability, life-history strategy, and limiting factors must be separated in explaining clutch size variation. Once separated, hypotheses about the effects of each may be developed and tested. Hypotheses about effects of food availability may be tested through measurement of energy intake rates of various species. Using life-history theory, clutch size differences attributable to variation in reproductive effort (e.g., Väisänen, 1977) can be related to factors such as life span (Boyd, 1962). Testing of hypotheses about limiting factors is even more promising. There are three substantial hypotheses: (1) egg-
formation ability, (2) incubation ability, and (3) parental behavior (different mechanisms for species that feed young and those that do not), all of which lead to specific predictions. An explicit parental behavior hypothesis was presented above, and the other hypotheses could be expanded to a similar level of specificity. Once specific predictions are formulated, these can be tested by experimental manipulations and further examination of clutch size variation so that hypotheses can be strengthened, modified, or eliminated. It is thus feasible to distinguish between these hypotheses.

Experimental manipulations are an especially promising research vehicle. In interpreting the results of these, one subtlety must always be borne in mind, namely the distinction between levels of explanation. One must specify whether a hypothesis explains proximate or ultimate limitation of clutch size. Often an explanation could function on either level, and it is imperative that levels be explicitly distinguished in the building of theories. This is a major problem in clutch size research.

There has been much speculating and broad generalizing, but it has yet to produce a consensus about the evolution of shorebird clutch sizes. The field awaits those willing to address specifics and to test hypotheses.

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APPENDIX: ETHOGRAM

<table>
<thead>
<tr>
<th>BEHAVIOR</th>
<th>DEFINITION</th>
</tr>
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<tbody>
<tr>
<td>Alert</td>
<td>Erect stance with neck extended and nearly perpendicular to the substrate, and trunk tilted downward posteriorly.</td>
</tr>
<tr>
<td>Rest-alert</td>
<td>Relaxed posture (see rest), but head held up and away from body.</td>
</tr>
<tr>
<td>Rest</td>
<td>All standing postures in which the head is tucked against the trunk; characterized by horizontal orientation of trunk, and often ruffled feathers and one-legged stance. Includes head tucked under wing.</td>
</tr>
<tr>
<td>Sit</td>
<td>All postures in which both legs are tucked under the body so that the trunk rests on the substrate, excepting incubation.</td>
</tr>
<tr>
<td>Forage</td>
<td>Includes a variety of postures involved in the capture and consumption of prey. These are characterized by an extended neck, and range from a nearly erect posture to one in which the neck extends toward the substrate while the trunk tilts upward posteriorly.</td>
</tr>
<tr>
<td>Walk</td>
<td>Distinguished from forage by absence of orientation toward substrate and absence of the usual pace exhibited when seeking food.</td>
</tr>
<tr>
<td>Preen</td>
<td>Cleaning and positioning feathers with bill.</td>
</tr>
<tr>
<td>Incubate</td>
<td>Sitting on or standing over eggs.</td>
</tr>
<tr>
<td>Active parental behaviors</td>
<td>See text.</td>
</tr>
<tr>
<td>Other</td>
<td>All behavior not included in above categories. Consists chiefly of drinking, bathing, flying, and social behavior.</td>
</tr>
</tbody>
</table>

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