

ANTI-PREDATORY BEHAVIOR OF LAPWINGS: FIELD EVIDENCE OF DISCRIMINATIVE ABILITIES

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ABSTRACT.—The responses of three species of lapwings (Charadriidae: *Vanellus* spp.) to various potential predators and physically similar non-predators were recorded in the field in Kenya and Venezuela to determine how responses varied with stimulus and context of encounter. Responses observed included various alarm calls, distraction displays, aggressive displays, and fleeing. Responses varied with location of predator (terrestrial or aerial) more consistently than with class of predator (mammal, bird, or reptile), although one lapwing species differentiated reptiles from other predators. Responses varied greatly with predator species and lapwing reproductive state. The results suggest that lapwings discriminate the various kinds of predators and non-predators they encounter and that responses to each correspond to the type and degree of danger each represents. Discriminative abilities appear to be more sophisticated, and false alarms much less frequent, than in domestic fowl, a difference that may be related to the more open nature of the habitats used by lapwings. Lapwings induced appropriate anti-predatory behavior from their chicks through alarm vocalizations. Except for a distinct call given to reptiles by one species, alarm vocalizations appeared to form a graded series. *Received 14 Nov. 1988, accepted 25 June 1989.*

Birds recognize their predators and respond to them in ways designed to avoid capture based on that recognition. The appropriate response varies with the species of predator and with the context of the encounter between prey and predator. Ideally a bird should avoid responding to species or individuals that do not pose a threat, and they should employ the response that will be most effective in each encounter with a dangerous individual. Such perfection, of course, is impossible to achieve. Available sensory information may be imperfect, and the stimulus situations that must be evaluated are almost infinite. Errors of different kinds have appreciably different costs: false alarms waste time and energy, but failure to respond to a predator may be fatal. How animals perceive and classify their predators and the threats that they represent is an interesting issue (Marler 1982). A related issue is the extent to which an individual may communicate its perceptions to others through responses such as alarm calls (Gyger et al. 1987).

That birds have sophisticated, complex predator recognition systems is readily evident. Countless species are known to respond to some predators with alarm calls that cause recipients to flee to cover or freeze, respond to others with calls that attract recipients and induce mobbing,

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and ignore yet others. Besides predator identity, response has been shown to vary with such aspects of the stimulus situation as stage of the reproductive cycle (Simmons 1955, Greig-Smith 1980, Patterson et al. 1980, Weatherhead 1982, Buitron 1983, Knight and Temple 1986) and predator behavior (Hamerstrom 1957, Morton and Shalter 1977, Shalter 1978). The means by which birds learn to recognize predators has been well studied by Curio (1975, Curio et al. 1978). What is lacking in the avian literature are quantitative studies of the relationships between stimulus situations and anti-predatory behavior (Gochfeld 1984) such as those on vervet monkeys (*Cercopithecus aethiops*) (Seyfarth and Cheney 1980; Seyfarth et al. 1980a, b) and ground squirrels (*Spermophilus* sp.) (Hennessy and Owings 1978; Leger and Owings 1978; Rowe and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981). Thus information about the total perceptual strategy, its limits, and its design is lacking. How do birds classify predators, taxonomically, by location (aerial or terrestrial), according to urgency of response (Owings and Hennessy 1984, Gyger et al. 1987) or by some other means? How fine may discriminations between dangerous predators and physically similar but non-threatening species be, and do species vary in this respect? How much information about predators is communicated between individuals? Do apparent errors such as false alarms represent errors in perception, or do they merely reflect the classification system used? Answering these questions requires a holistic approach to the study of predator recognition.

The pioneering study of Gyger et al. (1987) provides a framework for such research. Gyger et al. (1987) found that domestic fowl (*Gallus domesticus*) kept in large outdoor aviaries exhibited typical terrestrial and aerial alarm calls. Classification appeared to be based more on location of stimulus than identity of stimulus. False alarms were frequent. Detailed analysis of variation in aerial alarm calls led Gyger et al. (1987) to conclude that the first element of the call served an alerting function and that the second varied with the stimulus in a way that reflected the angular size of the object projected onto the retina of the bird. The strategy of domestic fowl appears to be to detect objects of a specific angular size travelling through the air rather than making fine discriminations between stimulus species. Gyger et al. (1987) relate this strategy to the presence of a visual system adapted for a broad field of view, a favorable feature in a ground-dwelling species.

The purpose of this paper is to present data from another group of ground-dwelling birds, lapwings (*Vanellus* spp.), that, similar to data from a passerine species (Buitron 1983), suggest a perceptual strategy that differs from that of domestic fowl. The paper provides a quantitative account

of the relationship between stimulus situations and responses to add to the growing body of literature in this area (Patterson et al. 1980, Buitron 1983, Byrkjedal 1987, Gyger et al. 1987, Trail 1987, Knight and Temple 1988).

METHODS

Study sites and study populations.—I observed Long-toed Lapwings (*Vanellus crassirostris*) and Blacksmith Plovers (*V. armatus*) in Amboseli National Park, Kenya during 14 months spanning three years (July–August 1975; August 1976–July 1977; December 1978). I observed Southern Lapwings (*V. chilensis*) near Mantecal, Venezuela during April–July 1978.

Amboseli and Mantecal both are areas of flat, open savanna. The climate in both sites is characterized by highly seasonal rainfall and lack of seasonality in temperature. Annual rainfall is much greater in Mantecal (1500 mm) than in Amboseli (300 mm). The study sites are described more fully by Ramia (1967), Altmann and Altmann (1970), Western and Van Praet (1973), Troth (1979), and Walters (1982).

Like most lapwings, the species studied are conspicuous ground-dwellers of open habitats. Long-toed Lapwings in Amboseli lived primarily on surface vegetation on marshes, whereas Blacksmith Plovers inhabited areas of short grass or sedge at the edges of marshes and waterholes. Southern Lapwings occupied habitat in Venezuela similar to that occupied by Blacksmith Plovers in Kenya. Most observations in Amboseli were made along Enkongo Narok Swamp, a permanent spring-fed body of water. Observations in Mantecal were made in privately owned cattle fields and in a government-owned livestock area containing many impoundments.

Sampling methods.—Based on ease of access and observability, I selected 10–20 pairs from each of the three lapwing populations for intensive observations. Sampling was rotated among these pairs so that all were sampled approximately equally often at all times of day. Pairs were identified by location (these are territorial species), and in the cases of Southern and Long-toed lapwings, by variations in plumage features.

Responses to predators were sampled by focal sampling (Altmann 1974), using a vehicle as a blind. Samples included one or two pairs of lapwings as subjects. Samples taken in Kenya were 15 min in duration, whereas those taken in Venezuela were 10 min in duration. Because these species are tame, conspicuous, and in open habitats, subjects were rarely out of sight during samples (4% of time in Venezuela, <1% in Kenya). Birds held territories long before and after breeding, so that responses of non-breeding territorial birds, as well as breeding birds, could be sampled.

I collected nearly 300 pair-hours of focal samples. I also collected ad lib samples (Altmann 1974) from flocks of non-territorial birds during both the breeding and non-breeding seasons and from pairs other than those intensively sampled throughout the breeding cycle. Because responses to predators were not apparently different during focal and ad lib samples, I combined the two kinds of data in the analyses, producing a sample of over 700 encounters with potential predators.

I considered all large reptiles, mammals, and birds to be potential predators for sampling purposes. Each time a potential predator entered the study area, I recorded the responses of the focal birds. I use Gochfeld's (1984) terminology to classify responses observed. When possible, I noted the distance between predator and responding bird when the response began, as well as the distance between the predator and any nest or young. I noted distances for each successive response elicited by a particular predator. Maps of the study areas facilitated estimating distance.

Recordings of alarm calls were made using Scotch tape 208, a Nagra III tape recorder,

and a Sennheiser MKH 804 directional microphone. Sound spectrograms were prepared on a Kay Sona-Graph 7029A using a wide-band filter.

RESULTS

Southern Lapwings

Response repertoire.—Lapwings appear to be exceptionally vigilant birds. Responses to those potential predators that evoked responses routinely began while the stimulus animal was well over 100 m from the birds. The initial response to a potential predator was often vigilant posturing and calling, but many encounters escalated to include more dramatic responses. Incubating birds regularly exhibited early surreptitious departure, quietly running from the nest in a crouched position. Other responses observed included two forms of attack, mobbing, crouched run, false brooding, injury-feigning, and ungulate display.

One of the forms of attack (pecking attack) also was limited to interactions with reptiles. In this display, the wings were held high as the bird struck at the potential predator with its bill and feet. The second form of attack consisted of swooping low over the stimulus animal. An odd click-like sound occurred as the bird passed over its victim, but I never observed the bird actually strike the victim. False brooding and crouched run were common responses, and the latter appeared to function as a distraction display. The performer was quite vocal and ran toward or parallel to the stimulus animal as well as away from it. Injury-feigning was rare and consisted of taking hobbling steps, either while dragging one trailing wing held out at an awkward angle, or while in a crouched posture with both wings spread. In the ungulate display, the bird spread its wings up over its back, exposing the boldly colored underwings, while standing in a slight crouch with its head held low. Often the bird lunged at the stimulus animal.

Vocalizations.—Behavioral responses typically were accompanied by vocalizations. Vigilant posturing was accompanied by a call employed in several other contexts such as when conspecifics approached the territory. This alerting call usually elicited no obvious response from chicks, if present, but sometimes induced very young chicks to crouch. Two additional alarm calls were given. The first (Fig. 1A) was commonly heard. It was given by birds standing in a vigilant posture and also accompanied crouched run, injury-feigning, false brooding, and swooping attack. This call appeared to grade into the alerting call. The individual notes sounded harsher, more intense and longer, with the ending less distinct than the notes of the alerting call. The notes of the alarm call may have been characterized by greater frequency modulation as well. By further changes in these same parameters, this alarm call graded into a call that attracted

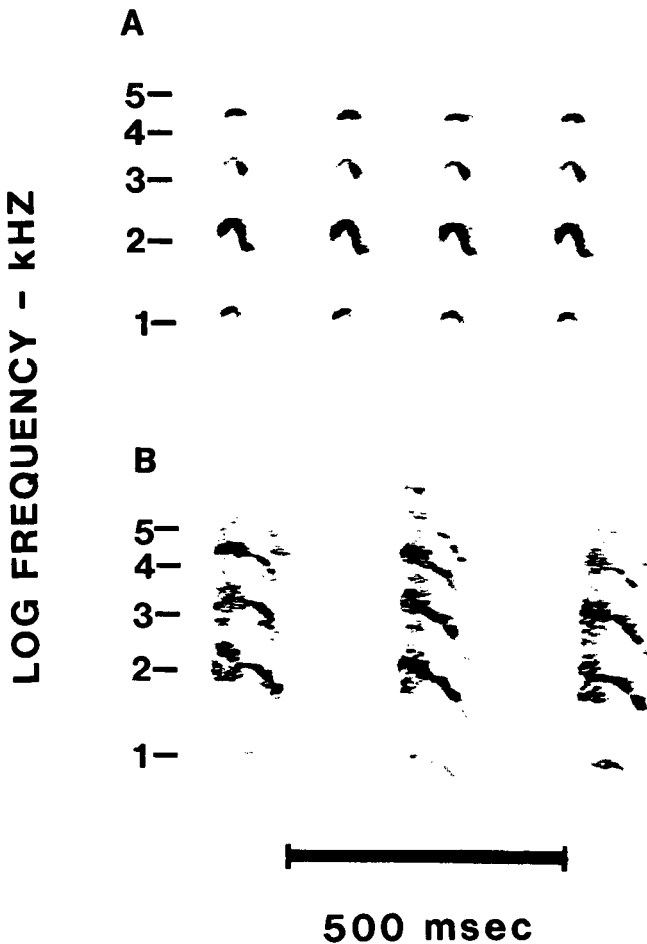


FIG. 1. Alarm call (A) and mobbing call (B) of the Southern Lapwing.

conspecifics to produce a mobbing response (Fig. 1B). It attracted not only territorial neighbors but also non-territorial vagrants, and all joined the calling birds in attacks, false brooding, crouched runs, and injury-feigning. When the danger passed, the residents vigorously evicted the attracted birds from their territory.

The first alarm call was bewilderingly variable. In addition to the variation involved in gradations with alerting and mobbing calls, there was variation in the pitch of the call and its tempo. I did not obtain sufficient recordings to analyze this variation, structurally or functionally. That

chicks, out of sight of the potential predator, responded to some calls by crouching instantly and to others, invariably ones given to mammals, by first running to cover and then crouching, indicates that at least some of this variation may be functional.

The second alarm call (reptile alarm call) was heard infrequently and was not recorded. This call occurred only during interactions with reptiles, accompanying pecking attack, and caused chicks to move rapidly away from the source of the call and remain upright and alert. It sounded more like the call used by parents when leading young than like the other alarm calls.

Variation in response.—Southern Lapwings exhibited three distinct types of responses to potential predators which were marked by the following behaviors: (1) reptile alarm call and pecking attack, (2) alarm call, swooping attack, injury-feigning, and mobbing, and (3) ungulate display. Alerting calls and vigilant posturing sometimes preceded all three types of response, and crouched run and false brooding regularly accompanied all three. The potential predators eliciting the first and third types of responses corresponded to taxonomic groups. The first type of response was directed only toward reptiles, and it was the only type of response given toward reptiles (11 cases). The third type of response was given only toward cows (7 cases), and it was the only type of response given to cows.

I observed only birds tending chicks responding to reptiles. There was some indication that all reptile species were not responded to equally. By far the most intense response witnessed was during the only observed encounter with the large predatory lizard *Tupinambis*. The response included repeated pecking attack, much false brooding, and prolonged reptile alarm. In contrast, responses to spectacled caimans (*Caiman crocodilus*) and iguanas (*Iguana iguana*) consisted of sporadic reptile alarm and occasional false brooding.

I observed only incubating birds performing the type 3 response, and only in the immediate vicinity of the nest. The birds inhabited fields used for grazing cattle, and thus constantly encountered cattle but ignored them except when they were in the immediate vicinity of an active nest. Horses, although less numerous than cattle, were also frequently encountered by the birds, and they, too, were ignored. I did not observe horses in the immediate vicinity of an active nest, however. Once a group of horses ran toward a pair of birds tending downy young, eliciting a type 2 response. Twice, I observed pigs in the vicinity of birds tending young, and both times an intense type 2 response was given, although the pigs never approached closely. The contrast in responses indicates that pigs were not classified with cows and horses by lapwings.

A variety of avian and mammalian species elicited type 2 responses.

Although the behavior of chicks indicates that adult responses to terrestrial and aerial predators may differ, most likely in some aspect of alarm calling, I was unable to document this. Three variables affecting response were evident: (1) stage of the reproductive cycle, (2) location of the potential predator, and (3) species of potential predator. To analyze the results, I subdivided the data according to these three variables to the extent that sample size would permit. The reproductive stages used are: (1) incubation, (2) tending small young (unable to fly, age 1 day to 6–8 wk), (3) tending large young (able to fly, age 6–8 wk to 5 mo), (4) territorial (defending territory but without eggs or young). The predator location categories used are (1) on the ground or perched near the ground, (2) flying near (<25 m) the ground, and (3) flying or soaring high (>25 m) above the ground. The two commonly observed mammalian species, dogs and humans, could be analyzed individually, but avian predators had to be grouped into the following classes due to small sample sizes: (1) caracaras (*Polyborus plancus* and *Milvago chimachima*), (2) hawks and falcons (*Buteo albicaudatus*, *B. magnirostris*, *Buteogallus urubitinga*, *Busarellus nigricollis*, *Falco femoralis*), and (3) kites and vultures (*Elanus leucurus*, *Rostrhamus sociabilis*, *Coragyps atratus*, *Cathartes aura*, *C. burrovianus*). I divided encounters into those in which a clear alarm response occurred (alarm call, crouched run, false brooding, mobbing, swooping attack) and those in which no response or only responses that were not clearly an alarm (vigilant posture, alerting call) occurred. I compared responsiveness among stages, among predator location categories, and among species by Chi-square tests comparing the frequencies of clear alarm response and no alarm response.

Sample size for birds tending large young was insufficient (9 encounters) for detailed analysis. The few responses observed were similar to those given by adults tending small young in equivalent contexts. Sample size for the territorial stage was also small (30 encounters). Responsiveness generally was low in this stage, but clear alarm responses were given to humans (6 of 12 encounters), caracaras (3 of 4 encounters with *Polyborus*, 0 of 3 encounters with *Milvago*) and one species of hawk (*Buteogallus*, 1 of 1 encounters). Several species that regularly elicited a clear alarm response during other stages did not during the territorial stage (dogs, 2 encounters; other hawks and falcons, 4 encounters).

There were several species to which lapwings were more responsive when tending small young than when incubating (Table 1). These included dogs ($P < 0.05$) and hawks and falcons ($P < 0.001$, combining all predator location classes). Lapwings were equally responsive to caracaras and to humans, both on foot and on horseback, during these two stages, and were equally unresponsive to vulture and kites. The lapwings were more

TABLE 1
RESPONSES OF SOUTHERN LAPWINGS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator location	Predator type	Frequency of response	
			No clear alarm response	Clear alarm response
Incubation	Flying high	Caracaras	3	1
		Kites, vultures	10	0
		Hawks, falcons	6	0
	Flying low	Caracaras	3	4
		Kites, vultures	6	0
		Hawks, falcons	6	0
	Ground, perched	Caracaras	0	2
		Kites, vultures	5	0
		Hawks, falcons	6	0
		Dogs	7	3
		Humans on foot	15	24
		Humans on horseback	8	3
Tending small young	Flying high	Caracaras	3	4
		Kites, vultures	10	0
		Hawks, falcons	2	10
	Flying low	Caracaras	2	4
		Kites, vultures	12	5
		Hawks, falcons	0	4
	Ground, perched	Caracaras	0	10
		Kites, vultures	2	0
		Hawks, falcons	1	1
		Dogs	3	17
		Humans on foot	27	90
		Humans on horseback	6	10

responsive to caracaras on the ground or perched than caracaras in flight when tending small young ($P < 0.05$), and there was a trend in this same direction during incubation (Table 1). They were less responsive to vultures and kites flying high than vultures and kites flying low, perched or on the ground when tending small young ($P < 0.05$). They were equally unresponsive to hawks and falcons and vultures and kites regardless of predator location during incubation, and were equally responsive to hawks and falcons in all predator locations when tending small young.

The birds were not equally responsive to all avian species either during incubation or when tending small young ($P < 0.001$ in both cases, combining all predator location categories). They were more responsive to

caracaras than to all other species during incubation, and less responsive to vultures and kites than all other species when tending small young. These results were significant within predator location category for both the flying low ($P < 0.05$) and flying high ($P < 0.001$) categories. Although the lapwings tended to be more responsive to humans than to dogs during incubation (Table 1), this trend was not significant ($0.05 < P < 0.1$). The birds were more responsive to humans on foot than to humans on horseback during incubation ($P < 0.05$), but not when tending small young.

Long-toed Lapwings

Response repertoire.—Adult Long-toed Lapwings responded to potential predators in similar ways to Southern Lapwings, although their response repertoire was smaller. Like Southern Lapwings, Long-toed Lapwings exhibited vigilant posturing and an alerting call (Fig. 2A) that was given in many contexts in addition to encounters with predators. This call did not elicit crouching from chicks. More intense responses observed were alarm calling and swooping attack. Alarm calls elicited crouching from chicks. They appeared to grade into the alerting call, the notes being longer, louder, and more frequent than those characterizing the alerting call (Fig. 2B). Long-toed Lapwings also exhibited an escape response in which they flew out over the open water, hovering just above the surface or occasionally performing swift, twisting evasive flight.

Variation in response.—I again divide encounters into those that resulted in a clear alarm response (alarm calling, swooping attack) versus those that did not (no response, vigilant posturing and alerting call only). I separated escape responses from these as a third category. Long-toed Lapwings gave clear alarm responses only to avian predators. I observed four encounters with jackals (*Canis aureus* and *C. mesomelus*) and four encounters with Rock Pythons (*Python sebae*), and repeatedly approached the edges of Long-toed Lapwing territories myself, but witnessed no swooping attacks or alarm calling, or escape responses. Adults and chicks approached pythons swimming or resting in their territory, but their reaction in no way suggested mobbing. One chick sat, apparently sleeping, within 0.5 m of a python for nearly an hour.

Small sample sizes precluded detailed analysis of variation in response to avian predators (Table 2). Effect of predator location could not be examined, and for only one group, harriers (*Circus* spp.) could I test for variation among stages of the reproductive cycle. Long-toed Lapwings were highly responsive to harriers, giving either an alarm or escape response in nearly all encounters with them, but there was no difference in response between birds tending eggs or young and those without eggs or young (Table 2). Species of potential predator had a noticeable effect on

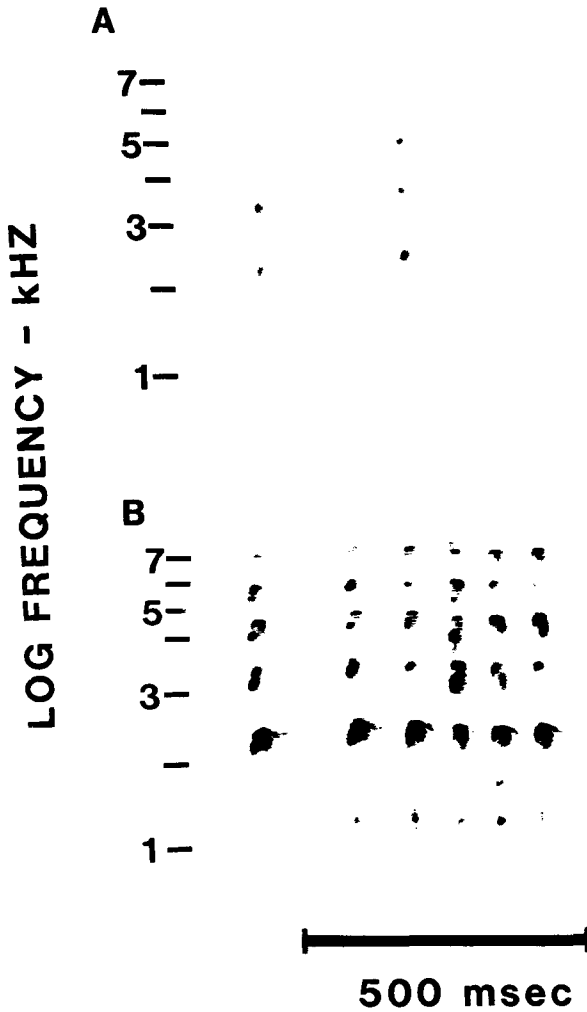


FIG. 2. Alerting call (A) and alarm call (B) of the Long-toed Lapwing.

response. The lapwings never gave a clear alarm or escape response to vultures (primarily *Gyps bengalensis* or five other species), although they were present soaring overhead so often that sampling encounters with them were unnecessary. The only clear alarm responses given to groups of circling vultures were to those few groups that included a Tawny Eagle (*Aquila rapax*) (Table 2). Long-toed Lapwings more often responded to harriers than to Fish Eagles (*Haliaeetus vocifer*) or harrier-eagles (primarily

TABLE 2
RESPONSES OF LONG-TOED LAPWINGS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator type	Frequency of response		
		No response	Alarm calling	Escape response
Tending eggs or young	Fish Eagle	3	2	0
	Harrier	1	17	6
	Falcon	0	2	3
	Tawny Eagle	0	1	0
	Harrier-Eagle	4	0	0
Not tending eggs or young	Fish Eagle	5	1	0
	Harrier	2	9	9
	Falcon	0	0	2
	Tawny Eagle	1	1	0
	Harrier-Eagle	7	0	0

Terathopis ecaudatus, or *Circaetus* spp.) both when tending eggs or young and when eggs and young were absent ($P < 0.05$ in all cases, combining clear alarm and escape responses). Although sample sizes were insufficient for analysis, the data hinted that falcons (large *Falco* spp.) and Tawny Eagles elicited responses more frequently than Fish Eagles or harrier-eagles (Table 2). I also observed encounters with kestrels (*Falco tinnunculus*) ($N = 2$), which were ignored, and White-browed Coucals (*Centropus superciliosus*) ($N = 3$) which elicited clear alarm responses.

Blacksmith Plovers

Response repertoire.—The responses exhibited by Blacksmith Plovers were similar to those observed in the other two species. Blacksmith Plovers employed vigilant posturing, an alerting call, an alarm call, swooping attack, crouched running, false brooding, ungulate display, and escape response. The form of all of these behaviors was similar to that described above for Southern Lapwings and Long-toed Lapwings. As in the other species, the alerting call and alarm call appeared to grade into one another (Fig. 3A and B). The latter, but not the former, induced the young to crouch, and the former was given in many contexts other than encounters with potential predators. In this species, a primary difference between the two calls appeared to be that the notes were shorter in the alarm call. There may have been functional variation among alarm calls as well. Notes of calls given to aerial predators (Fig. 3D) appeared to be even shorter than those of calls given to terrestrial predators (Fig. 3C). The number of calls recorded was not sufficient to investigate this variation.

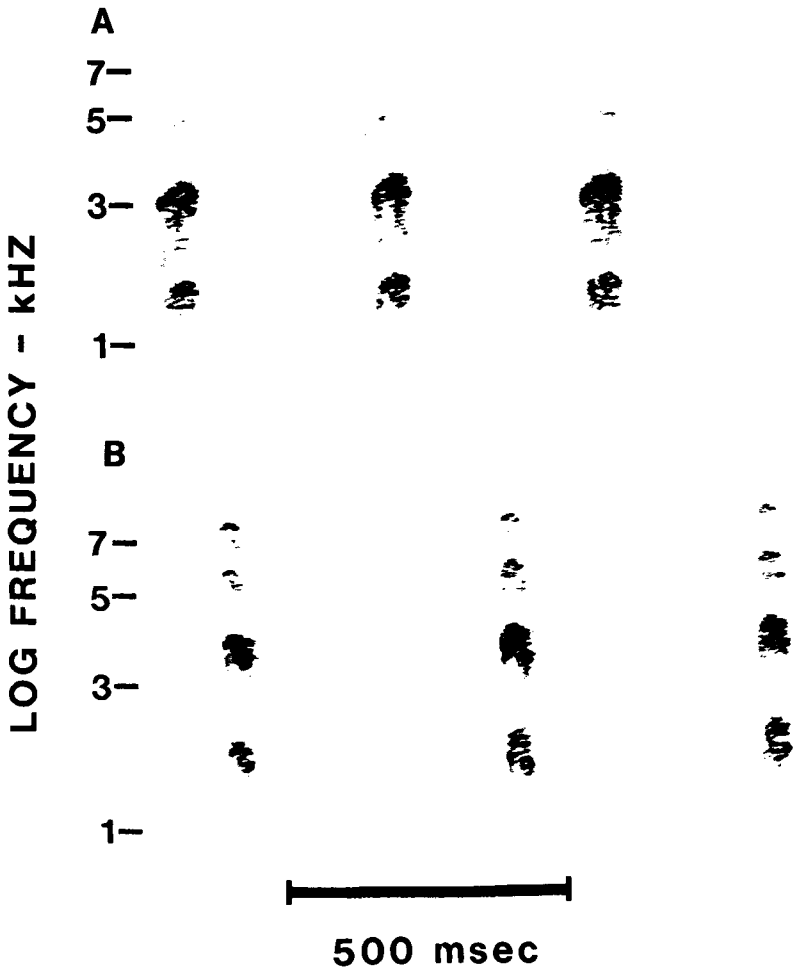
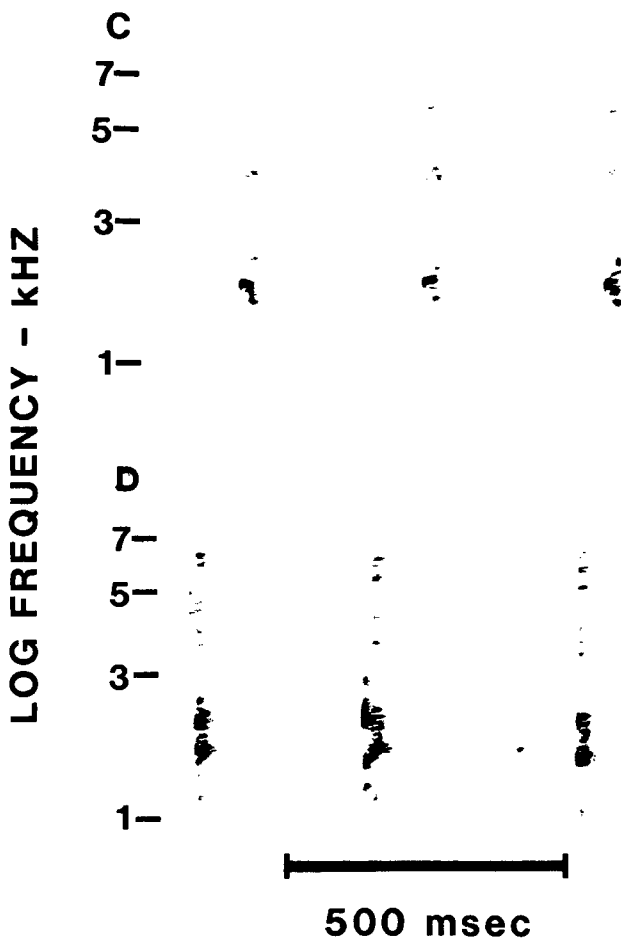


FIG. 3. Alerting call (A) and alarm call (B) of the Blacksmith Plover. (C) Alarm call given to a terrestrial predator. (D) Alarm call given to an aerial predator.

Variation in response. — Blacksmith Plovers exhibited three distinct types of response to potential predators: (1) ungulate display, (2) alarm responses characterized by alarm calling, swooping attack, and escape response, and (3) alarm responses characterized by alarm calling, crouched running, and false brooding. The third type of response was seen only in the three encounters with Rock Pythons observed. Other than these instances, I recorded crouched running and false brooding only in a few of the many



encounters with baboons (*Papio cynocephalus*) observed. Responses to baboons otherwise were type 2. None of the birds responding to rock pythons was tending eggs or young.

Only incubating birds performed ungulate display. I observed it directed toward wildebeest (*Connochaetes taurinus*) and toward me and received unconfirmed reports of responses to elephants (*Loxodonta africana*). Wildebeest were ignored by non-incubating birds. Non-incubating birds often ignored me, but those tending young gave alerting calls and led their young away from me.

Variation in alarm responses was more difficult to analyze than in other

TABLE 3
RESPONSES OF BLACKSMITH PLOVERS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator type	Frequency of response			
		No response	Alert calling or alarm calling	Swooping attack	Escape response
Tending eggs or young	Harrier-Eagle	3	8	0	0
	Fish Eagle	0	2	1	0
	Tawny Eagle	0	9	0	0
	Harrier	0	4	3	2
	Falcon	0	0	0	1
Not tending eggs or young	Harrier-Eagle	0	1	0	0
	Fish Eagle	9	0	2	0
	Tawny Eagle	1	1	0	0
	Harrier	6	2	5	1
	Falcon	0	0	0	1

species because it was harder to distinguish clearly alerting and alarm calls. Therefore, I do not separate responses that included only alerting calls from those that included alarm calling and distinguish responses that included swooping attack from those that included only alarm calling. Responses to terrestrial predators almost always included swooping attack in addition to calling. Encounters with terrestrial predators observed included one with a Secretary Bird (*Sagittarius serpentarius*), two with jackals, and innumerable encounters with baboons recorded during 1470 h spent following baboon groups while working on another research project. The attacks on jackals and many of those on baboons were performed by birds that were not tending eggs or young.

Like Long-toed Lapwings, Blacksmith Plovers generally ignored vultures which were overhead almost constantly. With only two exceptions, calling was elicited by only those groups of soaring birds that included a Tawny Eagle. Results of encounters with those aerial predators to which Blacksmith Plovers responded are presented in Table 3. Blacksmith Plovers were more responsive to both eagles ($P < 0.001$, combining all three types of eagle) and harriers ($P < 0.05$) when tending eggs or young than when without eggs or young. However, birds without eggs or young sometimes performed swooping attacks. Among birds tending young or eggs, responses to harriers differed from responses to eagles ($P < 0.05$), more often including swooping attack or escape response. This may have been due, at least in part, to a difference in predator location, as all harriers encountered were flying low, whereas 17 of 23 eagles encountered were

flying high. Responses to the two types of predators by birds without eggs or young were not significantly different. Falcons elicited escape response in both observed encounters, a response otherwise given only rarely in response to harriers (Table 3).

DISCUSSION

Predator Recognition Strategy

The perceptual strategy used by lapwings in predator recognition appears to differ substantially from that reported for domestic fowl by Gyger et al. (1987). Lapwings gave false alarms much more rarely and appeared to make finer discriminations among stimulus species. Although more data are needed to substantiate many apparent trends, it appears that variation in lapwing responses matches rather precisely variation in the danger represented by different stimulus contexts (see below). In this respect, it appears similar to the strategy of vervet monkeys (Seyfarth and Cheney 1980; Seyfarth et al. 1980a, b) and ground squirrels (Hennessy and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981; Owings and Hennessy 1984). The lapwing strategy seems to be to assess accurately each stimulus situation and then respond accordingly. Response time under this strategy presumably is slower than that under the strategy of the domestic fowl, which emphasizes rapid detection over a broad field of view. I suggest that this difference in strategy is related to differences between the two kinds of birds in the nature of interactions with predators. The wild ancestors of domestic fowl inhabited places in which obscuring vegetation limited their visual range. Furthermore, ground-dwelling phasianids rely on reaching cover rather than maneuverability in the air to escape predators. The cost of a false alarm in this species is presumably small because encounters with predators are brief. On the other hand, the consequences of failing to respond quickly to a predator may be fatal, because little time exists in which to correct the mistake, and delays in responding greatly reduce ability to escape. A response strategy that emphasizes quick response at the expense of fine discrimination might characterize most species living in closed environments, such as forests, for similar reasons. Trail (1987) reports a high frequency of false alarms in Cock-of-the-Rock (*Rupicola rupicola*), a species that inhabits dense forest.

The lapwings studied, on the other hand, typically have a long visual range unimpeded by vegetation in the environments in which they are found. Large birds in flight are almost constantly in view, and most can be seen long before they come within attacking distance. False alarms in such environments would be frequent and prolonged, and therefore costly,

whereas the consequences of failing to respond to a predator immediately are trivial because ample time exists to correct the mistake. In addition, lapwings are sufficiently strong fliers that they likely can escape most predators in flight, and thus allow them a closer approach than can domestic fowl. A perceptual strategy that minimizes false alarms appears well suited for species with such a life history. Buitron (1983) provides data from another species of open country, the Black-billed Magpie (*Pica pica*), that suggest an anti-predatory strategy similar to that of lapwings. She also documents fine discriminations within classes of predators and apparently adaptive changes in responses to particular species over the breeding cycle.

Lapwings appear to classify potential predators by a combination of taxonomic and urgency of response criteria. Southern Lapwings distinguished reptiles from non-reptiles, and Long-toed Lapwings were unresponsive to mammals. On the other hand, Southern Lapwings responded similarly to mammal and bird species, as did Blacksmith Plovers. In these latter cases, although the general response to different taxa was similar, additional taxonomic distinctions could have been expressed in variation in alarm calls that I could not perceive. Many discriminations made by lapwings are difficult to reconcile with any means of classification based on generalization of taxonomic cues, however. For example, Southern Lapwings responded to pigs and cows very differently, yet responded to my vehicle in the same manner as to cows. These observations are more consistent with a scheme in which species are identified individually and classified according to an urgency of response scheme. For example, a scheme consistent with my observations is that any species will elicit an ungulate response if it approaches a nest closely; others (e.g., vultures) will elicit an alarm response only if in the immediate vicinity of the young, while others will elicit an alarm response at long distances.

Adaptive Nature of Variation in Response

Variation in type of response.—Evidence of an adaptive match between response and stimulus context exists in several aspects of variation in response to potential predators. The species that elicited only ungulate display were herbivorous species that might step on and crush eggs or small young but otherwise were no threat to lapwings. Pigs, on the other hand, elicited an alarm response. This may represent a false response, but pigs are omnivores and it is conceivable that they might consume lapwing eggs or even small chicks. That a shorebird could be as unresponsive to mammalian predators as Long-toed Lapwings appeared to be is extraordinary, yet this too may be adaptive, since mammals may pose no threat to a species that inhabits surface vegetation over water. Southern Lapwing

chicks responded to reptile alarm by remaining mobile and alert, a more appropriate response than the crouching elicited by the usual alarm call because reptiles could more easily locate and capture a stationary chick than a moving one.

If the response system of lapwings is as fine-tuned as I suggest, one expects to find a difference in response to terrestrial and aerial predators. Although lapwings do not have distinct alarm calls for terrestrial and aerial predators as many birds do, it is possible that some of the apparent variation in alarm call structure differentiates terrestrial and aerial predators.

Variation among species of potential predator.—Without accurate information about the diets of the species of potential predators, it is difficult to determine whether variation in lapwing response accurately reflects variation in the threat posed by the various predator species. Only baboons were actually observed preying on lapwing eggs, and no species was observed to take chicks or adults. The diets of the potential predators are known only in general terms (Steyn 1965, 1973; Brown and Amadon 1968; Voous 1970; Brown 1971; Smeenk 1974; Picozzi 1978). Considering the general foraging habits of the species involved, nothing I observed is inconsistent with the hypothesis that lapwings are able to identify each species of potential predator that they encounter and respond to it precisely according to the danger it represents to them. Vultures and kites are unlikely to prey on eggs, young, or adults, and lapwings generally ignored them, responding to them only when they flew very close to chicks. Species to which the lapwings responded strongly, such as caracaras, falcons, and harriers are likely predators of lapwings. Southern Lapwings ignored the fish-eating specialist *Busarellus nigricollis* but responded strongly to other large hawks.

That lapwing responses accurately reflect the danger a particular potential predator poses requires several suppositions that are not obvious from what is known of the general foraging habits of the predators. Humans in Africa must be much less inclined to harm lapwings and their eggs and young than humans in Venezuela. Harrier-eagles and Fish Eagles must not be a threat to Long-toed Lapwings, whereas Tawny Eagles must be. Variation in response might also reflect variation in the effectiveness or risk of the response across predator species (Simmons 1955, Elliot 1985, Knight and Temple 1988). In this study, these aspects likely affect the form of the response, and unmeasured details such as approach distance, but not the consistency of response. That is, those species that were ignored do not appear to be sufficiently different from those to which the lapwings responded that increased risk or decreased effectiveness could have inhibited responding.

Some of the variation in response among predator species requires considerable discriminatory abilities. For example, the African species ignored vultures, yet responded to Tawny Eagles, which are similar to vultures physically and in flight pattern and often fly with them. That lapwings may possess unusual abilities in this regard has been suggested by others (Meinertzhagen 1954, Bannerman 1961). But evidence is mounting that many species may make such subtle discriminations in their anti-predatory behavior (Zimmerman 1976, Ficken and Witkin 1977, Grubb 1977, Buitron 1983, Bump 1986), although some species appear to be poor discriminators (Mueller 1976).

How such subtle discriminations might be learned is an interesting issue. Associative learning is one possible mechanism. In this regard, the behavior of lapwings in zoological parks may be revealing. At the Lincoln Park Zoo in Chicago, Spurwing Plovers (*V. spinosus*) have learned to distinguish zookeepers who take their eggs from other humans (K. Bell pers. comm.). They attack the uniformed keepers the moment they enter their large aviary, whereas they ignore zoo visitors passing within a few meters of their nest. But associative learning is too dangerous a mechanism for developing some of the discriminations exhibited by lapwings. Cultural transmission of predator recognition, which has been demonstrated in other birds (Curio et al. 1978), is a likely, less risky alternative.

Variation over the reproductive cycle.—Considerations related to parental investment may account for some variation in responsiveness to predators over the reproductive cycle (Knight and Temple 1986). But neither this nor any other general change in motivation (Simmons 1955) can account for changes in responsiveness that are not uniform across predator species. That changes in responsiveness to predators across reproductive stages match dangers posed by predators has been reported previously (Patterson et al. 1980, Buitron 1983). In this study, Southern Lapwings became more responsive to species likely to take young but not eggs (hawks, falcons, possibly dogs) when their eggs hatched, but began responding to those species that are likely to take eggs (humans, caracaras) during incubation. Caracaras are notorious scavengers, and humans in the region of the study consume lapwing eggs. It is also interesting that non-breeding Southern Lapwings remained responsive only to caracaras, which are known to prey on adults (Myers 1978), and humans who frequently threw rocks at adults.

Long-toed Lapwings and Blacksmith Plovers remained more responsive to a greater variety of species when not breeding than did Southern Lapwings. Perhaps most of these species prey on adult lapwings, but this is unlikely for at least some species, for example, baboons. Baboons regularly elicited intense versions of responses such as false brooding, normally associated with breeding, from birds that were not even holding a territory.

Perhaps these responses are non-functional mistakes. Another hypothesis is that such behavior disguises the presence of young from an intelligent predator. I also observed Crowned Lapwings (*Vanellus coronatus*), another lapwing species in Amboseli subject to baboon predation, to direct elaborate anti-predatory behavior at baboons when not breeding.

Communication Between Adults and Chicks

Part of the anti-predatory behavior of lapwings is to communicate, through vocalizations, information that enables chicks to take appropriate action. All species studied employed alarm calls that induced young to crouch, and Southern Lapwings gave an additional reptile alarm call that triggered evasive action by chicks. The dichotomous signal-response system of Southern Lapwings may represent semantic communication (Altmann 1967; Seyfarth et al. 1980a, b). Otherwise, there was no obvious communication of predator identity.

Lack of discrete calls does not necessarily mean that communication of alarm is simple, however. The graded vocalizations of lapwings in theory permit elaborate communication between adults and young. Gradations in alarm calls given by ground squirrels provide information about predator identity and subtleties of context that reflect degree of danger, and there is evidence that recipients use this information to vary their response to alarm in an adaptive manner (Leger and Owings 1978; Rowe and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981). The communication between adult lapwings and their chicks may be equally complex. A similar potential has been suggested for graded alarm vocalizations in Carolina Wrens (*Thryothorus ludovicianus*) (Morton and Shalter 1977) and exists for many other species (Buitron 1983, Brown 1985, Knight and Temple 1988), but such communication has yet to be demonstrated in birds. There were hints of it in the responses of Southern Lapwing chicks to alarm calls. Young consistently ran to cover before crouching when adults gave alarm calls to terrestrial predators, but they crouched immediately when adults gave alarm calls to aerial predators, even when the chicks themselves could not possibly see the predator. A detailed spectrographic analysis of lapwing alarm vocalizations will be necessary to determine if this response difference corresponds to vocal gradations. Graded systems such as these are common in birds (Adret 1982), and determining their functional significance is a major outstanding research problem (Miller 1979).

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