PREDATION AS A SELECTIVE FORCE ON FORAGING HERONS: EFFECTS OF PLUMAGE COLOR AND FLOCKING

GLORIA S. CALDWELL[1]

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

ABSTRACT.—Experiments using model herons in natural mangrove habitats demonstrated that more hawks are attracted to white than to blue herons. Both Common Black-Hawks (*Buteogallus anthracinus*) and crocodiles (*Crocodylus acutus*) were observed preying on adult herons in Panama. Solitary herons were at greater risk than flocked foragers. White (immature) Little Blue Herons (*Egretta caerulea*) were attacked more frequently by hawks than were the blue adults of their species. Dark herons gave more alarms than white herons. Although flock size decreased in years of heavy predation and after attacks, mixed-flock composition remained the same. When flocks re-formed after hawk attacks, their members showed decreased foraging rates and increased interindividual distances. After repeated attacks, herons foraged in poorer habitats, under unfavorable climatic conditions, and under thermoregulatory stress. These results suggest that predation could be a potent force in maintaining color dimorphism in ardeids. *Received 26 December 1984, accepted 7 January 1986.*

SEVEN species of herons share a color dimorphism in which individuals of both sexes are either white or some shade of gray or blue-gray (Hancock and Kushlan 1984). In one species, the Little Blue Heron (*Egretta caerulea*), the dimorphism is age-related. Individuals are white until the end of their first year, at which time they molt to a slaty blue plumage (Rodgers 1980). Individuals of the other species retain either white or blue-gray plumage throughout their postfledging lifetimes. Despite the prevalence of these dimorphisms, little is known about the selective forces that maintain them.

In similar color polymorphisms in other species, differential predation has been shown to be a potent selective force (e.g. Jones et al. 1977, Endler 1978). Despite this and despite the suggested importance of predation to bird coloration in general (e.g. Baker and Parker 1979), predation has been discounted as an important selective pressure on adult herons, whether dimorphic or not (Milstein et al. 1970; Murton 1971; Recher 1972; Holyoak 1973; Kushlan 1977, 1978; Mock 1981; but see Harvey 1975). However, most research on herons has centered on temperate breeding colonies, where the availability of eggs and nestlings makes adults less likely targets for predation, and where preda-

tors large enough to consume adult herons have not been abundant for some time. Even in temperate regions, however, there have been scattered reports of predation on adult herons (Baldwin 1940, Monson 1951, Cottrille and Cottrille 1958, Hancock and Elliott 1978, Robertson 1978, Graham 1984, Richter 1985, M. England pers. comm.), but these have been largely anecdotal or circumstantial. The lack of statistically meaningful data on natural predation on adult herons is not unexpected: natural predation on mobile animals is notoriously difficult to observe (Endler 1978). Predators large enough to eat adult herons are wary of animals as large as human observers.

In the course of studying foraging herons in the tropics (e.g. Caldwell 1981), I have seen many predatory attacks on adult herons, primarily by crocodiles (*Crocodylus acutus*) and by the Common Black-Hawk (*Buteogallus anthracinus*). Both resident tropical herons and herons that migrate to the tropics during the northern winter must contend with the risk of predatory attack that exists in many areas of the tropics. In this paper, I present details of the observed attacks and examine some indirect effects that even unsuccessful attacks have on a heron's fitness. The changes in heron flock structure associated with natural predatory attacks are compared with those observed in other flocks (e.g. reviews in Pulliam and Millikan 1982, Myers 1984) and with theoretical predictions

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[1] Present address: Department of Zoology, University of California, Berkeley, California 94720 USA.

(e.g. Treisman 1975, Rubenstein 1978). I also report the results of a field experiment designed to assess the differential risk from predation faced by herons of different colors in the Neotropics, and discuss the effect that differential predation might have in maintaining color dimorphism in ardeids.

STUDY AREA AND METHODS

Study area and populations.—Observations and field experiments were conducted on herons foraging in Panama, with special emphasis on Little Blue Herons. Little Blue Herons are dimorphic, and both morphs share the same geographical distribution. Because they have an age-dependent polymorphism, color does not reflect differing genotypic adaptations to local geographic locations, although correspondence of microhabitat and color still would be possible. Because Blue Little Herons generally do not breed until they have molted into the blue plumage (Rodgers 1980), each individual probably has been subjected to the selective factors affecting both white and blue plumage by the time it has bred successfully.

In Panama, large mixed-species flocks consisting of resident and migrant Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Tricolored Herons (*E. tricolor*), and occasional Green-backed (*Butorides striatus*) and Great Blue herons (*Ardea herodias*) are common from November through January (Caldwell 1981). Smaller mixed flocks occur at other times of the year, especially at foraging sites near breeding colonies. All species within these flocks eat the same food. However, flock members of all species are attracted to Snowy Egrets, rather than to the food (Caldwell 1981). Flocks were observed in December 1975, from January 1977 through January 1978, and from November 1982 to November 1983, for a total of 2,100 h of observation. In normal years, as in 1977, most resident Great and Snowy egrets leave sites on the Atlantic coast in early February for breeding sites on the Pacific coast, where they feed on seasonally abundant fish associated with the upwelling that normally occurs in the Bay of Panama during the dry season (January through March). The egrets do not return until summer. In February 1983, however, they repeatedly left for 2-3 days at a time, but returned to Atlantic sites and remained there through March. This was an unusual year because the normal upwelling in the Bay of Panama did not occur, presumably due to the effects of El Niño. Consequently, fewer fish were available for egrets in the Bay. Very few egrets attempted to breed in the Bay of Panama in 1983, nor were they observed breeding elsewhere. Little Blue Herons, however, bred in scattered sites in the mangroves on the Atlantic coast in April of all years.

Field observations.—Natural flocks and solitary herons foraging in mangroves and on adjacent beaches and coral reefs on the Atlantic coast of Panama were observed from a blind, usually an automobile, with the aid of binoculars and a Balscope zoom telescope. Herons most often foraged on a series of inlets into mangroves on Galeta Island, approximately 2 km from their roost. When the herons were absent, a stretch of coastline approximately 45 km in length was searched. It contained similar, but slightly more disturbed, habitat and stretched from Galeta Island to Ft. Sherman in the Province of Colon. Nearby areas further inland were more populated by humans and supported few herons. During this time the distribution of all herons in the area, flock size and composition, and predatory attempts were noted; foraging rates, aggression, alarm calls, and alert postures were sampled by the focal-animal method (Altmann 1974). For each focal animal the distances to the nearest individuals of each species in the flock were estimated by comparison to known body lengths of birds. The shortest distance was the nearest-neighbor distance for that individual. The mean of all nearest-neighbor distances for all the focal individuals in that flock was then taken to estimate flock cohesion.

The flocks in the mangroves and deforested inlets usually were arranged longitudinally along both sides of the channel of water. The mangrove inlets were covered with canopy, except near one end that opened onto a road or to the ocean. In this study, the most peripheral herons in the mangroves were defined as the 5 birds closest to the open end. Typically, these birds were more exposed to detection by aerial predators; these birds, however, were not necessarily at higher risk than others in the same flock, because the black-hawks used the canopy to conceal their approach. On the reef the geometric shapes of the flock were more variable, dependent upon resource distribution and water depth. The shapes of the flocks on the reefs were seldom simple, and thus I did not attempt to define the most peripheral birds there.

When a flock was disrupted by a predator, random individuals from that flock were followed whenever possible until they either roosted or began foraging again, whereupon they were observed again. If they returned to the roost or could not be found, foraging sites in the area were checked throughout that day to determine whether and where the flock, or parts of it, re-formed. All the foraging sites in the area were known, so it was not difficult to relocate flocks when they formed. The herons, crocodiles, and hawks in the area were accustomed to automobiles. Although being in an automobile may have facilitated observations of predation, it was not always essential. Black-hawks were quite bold: on one occasion, a hawk swooped within 1 m of an observer to attack a heron, and several attacks by hawks were observed by chance in 1983 by humans without blinds.

To define differences in habitat associated with predatory attacks, and to help differentiate between the effects of resource availability and the effects of predation, habitats were compared in years of heavy and light predation, and before and after predatory attacks. For these comparisons, habitats were classified with respect to amount of canopy, reef or mangrove substrate, wind speed, and abundance of fish. Percentage of canopy was measured with a spherical densiometer (Lemmon 1957). Wind speed was measured with an anemometer positioned where herons had been foraging. Fish abundance was determined using an underwater video camera.

When data from naturally foraging white and dark herons are compared, Great Egrets, Snowy Egrets, and immature Little Blue Herons are classified as white, whereas adult Little Blue Herons, Tricolored Herons, and Green Herons are classified as dark. Data from molting Little Blue Herons were not included in this study because of the problem of classifying a continuous variable. Fewer than 9% of the Little Blue Herons were molting at any one time.

Field experiments.—Model Little Blue Herons were constructed of polyurethane foam (Caldwell 1981) in a mold cast from a heron in an upright feeding posture. The models were painted to resemble white and blue morphs of the Little Blue Heron. Individual models were placed within 0.5 m of each other to form a flock. I used flocks because I felt that they would be more effective than one model in attracting predators, and because most of the natural attacks by hawks were on flocking herons. A flock of 5 white models and a flock of 5 blue models were placed at least 30 m apart in 24 different mangrove and reef sites along the Atlantic coast of Panama. The distance between the flocks was necessary to distinguish which flock had attracted the hawk. Experimental sites were chosen because Little Blue Herons were known to feed there, because black-hawks were seen in the area, and because the two areas where the flocks were placed could be watched from the same point, usually a road. The mangrove sites all had dark mud substrates. All sites were at least 1 km apart and took advantage of the natural spacing of different hawks. These hawks appeared to have regular foraging ranges with distinct boundaries. No hawk was seen to cross one of these boundaries. The occupants of different ranges frequently called and displayed to each other at the boundaries, so it was not difficult to determine which areas were the domains of different hawks. Thus, each experimental site was in a different foraging range, even though certain ranges were patrolled by more than one hawk, usually an adult and a juvenile.

Each trial began at approximately 0800, because most hawk attacks on real herons occurred between 0800 and 1000. During each trial the flocks were observed from a blind for 2 h or until a predator approached. The flocks were far enough apart to determine easily which flock had attracted the hawk. An avian predator was scored as approaching a flock if it made an aborted swooping attack on a member of that flock or if it landed in a tree directly over a flock, focusing on the flock. Black-hawks usually initiated attacks on real birds from such perches. On the day following each trial, the trial was repeated in the same site with the positions of the white and blue flocks reversed to control for position effects. Hawks never came to the same position on the two consecutive days. Several times, however, a hawk came to the same-colored flock in different positions on the two successive days in a site. This was counted as only one approach because it was not always possible to discriminate different hawks within a site. Several times two hawks, usually an adult and a brown-plumaged juvenile, came together. One usually circled above the flock while the other attacked. If more than one hawk approached a flock on the same day, it was counted as only one approach because the events were probably not independent.

During each trial, both flocks, the sky overhead, and the surrounding trees were scanned continuously with the aid of binoculars. If real herons came into the area before the hawks appeared, they were scared away by the observer so that the hawks would not be influenced by their presence.

The trials were conducted from November 1982 until July 1983. This spanned both rainy and dry seasons, although trials were conducted only when it was not raining. The response to the model birds did not appear to differ by season, even though crabs, an alternative prey for Common Black-Hawks, were much more abundant above ground during the rainy season.

RESULTS

FIELD EXPERIMENTS

Significantly more hawks were attracted to the white than to the blue model flock (15 hawks attracted to white models vs. 1 to blue models; $P < 0.001$, binomial test). In the one case when a hawk approached the blue flock, the hawk had flown in from behind the blue flock. There were trees separating the two flocks, and it is unlikely that the white flock was ever in its line of sight.

The attraction was unambiguous, even though the hawks never actually made contact with the model birds. When the terrain was open, the hawks made swooping attacks, but abruptly aborted these attacks 1–2 m from the models. When there were trees close to the

TABLE 1. Predatory attacks and successful captures
by hawks on foraging adult herons.

	Flocked foragers	Solitary foragers
Attacks	24	11
Captures	2	3

flocks, the hawks flew silently through the can-
opy, where they were well camouflaged, and
landed in the tree closest to one flock, focusing
on that flock. Once there, however, the hawks
often looked around. It occasionally was ap-
parent that at that time they also saw the sec-
ond flock: some hawks then did a series of head-
turning movements, where they alternately
oriented their heads toward one and then the
other flock, focusing on each flock for approx-
imately 1 s before switching back to the other.
Other hawks cocked their heads back and forth,
but looked at only one flock for up to 5 min
before flying away. From the hawks' perches
in the trees, they apparently could distinguish
real from model birds, because, with one ex-
ception, hawks did not approach beyond this
point. The exception occurred when a real her-
on approached the white flock after a hawk had
landed, and the hawk attacked but missed the
real bird.

FIELD OBSERVATIONS

Risk of solitary vs. flocked foraging.—Common
Black-Hawks made 35 observed attacks on adult
herons in 1982–1983 (Table 1), whereas in 1975–
1978 the black-hawks in the area were never
observed attacking herons. The reason for the
dramatic difference between years is not ob-
vious, but it was associated with large fluctua-
tions in the availability of land crabs, an alter-
native prey. The hawks actually captured the
herons in only 5 of these attacks. Several other
instances were near misses, but the herons
flushed before the hawk made physical contact.
Only once did a hawk pursue a heron after the
heron had taken flight, but it did not capture
the heron. In one instance a Green-backed Her-
on that had been captured escaped from the
hawk's talons when the hawk landed on a perch
about 200 m from the capture site. Because, in
this study, I had to observe the actual predatory
act to classify it as hawk predation, a few high-

ly probable cases were not included. In one,
for example, as I was approaching an area where
solitary herons often foraged, I saw a hawk flush
from the ground. There I found a newly dead
Great Egret with a broken neck. Because I could
not be positive that the hawk had not been
attracted to an already dead egret, this and six
similar instances were not included in the cal-
culations. Including them would not have
changed the outcome.

During October through February 1982 and
1983, herons fed in flocks 92% of the time. Thus,
the observed pattern of hawk attacks on soli-
tary vs. flocked herons (Table 1) during the
months when flocks were common in the area
deviates significantly ($\chi^2 = 26.09$, $P < 0.001$)
from the abundance of birds observed foraging
under each condition. An individual heron runs
a greater risk of being attacked by a hawk when
it forages alone than when it flocks, even
though the flocks are attacked more frequently
than individual birds. This calculation of risk
assumes that only one bird was the focus of
attack, even though that bird may have been
in a flock. Because a hawk can capture only one
heron per attack, this is a reasonable assump-
tion.

Trying to assess relative risks of solitary vs.
flocked foraging for members of any individ-
ual species or morph is difficult because of the
problem of identifying the target of an attack
within a flock. Among flocked foragers, the tar-
gets could not be discerned accurately unless
the birds were captured or the attack was a near
miss. The two captured herons (Table 1) were
Snowy Egrets (which constituted 60% of flock
participants). The one discernible near miss in
a flock was an immature Little Blue Heron
(which constituted 4.5% of flock members.) The
other attacks were in regions of the flock where
Snowy and Great egrets were most numerous,
but the exact targets could not be discerned.
Thus, while there could be a tendency to attack
white birds, which were in the majority, rather
than "odd" or minority individuals (22% of the
flock was dark), the data are too few to dem-
onstrate that hawks attacked members of par-
ticular species or colors in any way other than
at random within the mixed flocks. Assuming
that the nondiscernible targets within the flocks
were random, the relative risks of solitary vs.
flocked foraging can be calculated for members
of some individual species and morphs, know-

ing the numbers of each observed for standard time periods under each condition. Tricolored and Little Blue herons were the targets of predatory attacks significantly more often when foraging alone than when foraging in a flock ($P = 0.006$ for Tricolored and $P = 0.04$ for Little Blue herons, Fisher test). Immature Little Blue Herons were the target of attack significantly more often when they foraged alone ($P = 0.04$, Fisher test), but adults were attacked too infrequently for adequate comparison of the risks of flocked and solitary foraging. Snowy and Great egrets foraged alone too rarely for adequate comparisons of solitary vs. flocked risk.

Based on the number of successful captures, a heron foraging alone ran a significantly greater chance of actually being eaten than did a heron foraging in a flock ($P = 0.02$, Fisher exact probability test). These data on successful captures may be misleading, however, because they grouped all species of herons together, and members of some species evaded attacks better than members of other species.

Hawk attacks on solitary foragers.—Among solitary foragers, Tricolored Herons were attacked most often (Table 2), but Green-backed Herons were the only solitary foragers observed being captured. Relative risks differed for individuals of certain species and for morphs within species, both in probability of being attacked and in probability of being successfully captured. When hawks attacked solitary herons, they did not attack in proportion to the abundance of each species or morph (Table 2). Adult Little Blue Herons constituted 55% of the solitary herons foraging but only 12.5% of the attacks, thus eliciting significantly fewer attacks ($P = 0.003$, Fisher test) than would be expected; immature Little Blue Herons constituted 21% of the solitary herons but 37.5% of the solitary herons attacked. Comparison of the relative number of attacks revealed that the white morph ran a greater risk of being attacked than did the blue adult Little Blue Heron ($P = 0.07$ for solitary birds, $P = 0.03$ for solitary and flocked birds combined; Fisher exact probability test).

Tricolored Herons elicited more predatory attempts than expected on the basis of their abundance as solitary foragers ($P = 0.02$, Fisher test), and perhaps more than expected based on the results of the model experiments or the similarity of their dorsal coloration to that of

TABLE 2. Attacks by hawks on solitary herons of different species and morphs in relationship to their abundance as solitary foragers.

	Little Blue Heron		Tri-colored Heron	Other species combined
	Adult	Immature		
Herons observed	136	52	27	32
Attacks	1	3	4	3
Successful captures	0	0	0	3

adult Little Blue Herons. However, a hawk probably first would view a heron not from directly overhead but from a distance and at an angle where it might see the side, or even the front, of the bird. White patches are visible from the sides and front of Tricolored Herons, and could be even more apparent with movement. The swift strikes of a heron catching fish might be especially likely to catch the attention of a predator if they involved flashes of white contrasted against a dark background.

Nonlethal effects of hawk attacks on flock participants.—The number and identity of species in the mixed flocks remained the same in years of heavy and light raptorial predation and before and after attacks. The proportion of white vs. dark birds in the flocks also remained approximately the same (Table 3), so there was no tendency for increased homogeneity of the flocks after attacks. The mean number of flocks in the area did not change significantly, although there was a noticeable effect on variance. During the winter months of 1975–1978, only one flock formed every (nonrainy) day in the area, whereas during the same months in 1982–1983, there were many days when no flocks formed in the area, and days when 2 or 3 simultaneous flocks formed (mean number of flocks = 1.27 ± 0.14). After attacks, the variance increased ($P < 0.05$, Levene's test; Van Valen 1978), with some flocks splintering into smaller flocks and many never forming again (mean number of flocks = 0.82 ± 0.26) on that day. On days when flocks could not be found in the area, there was no large increase in the number of birds foraging solitarily. After attacks, when flocks did not reform, there was a small increase in the number of scattered individuals feeding at odd times and places, but they did not compensate for the number of individuals the predator had disturbed.

Within the flocks, nearest-neighbor distances increased slightly after attacks (Table 3), indicating that the flocks did not become denser after the attacks. The flocks were significantly tighter in the years with no observed raptorial predation than in the years with raptorial predation (Mann-Whitney $U = 18999$, $P < 0.001$). The mean nearest-neighbor distance within flocks on days hawks attacked (Table 3) was slightly, but not significantly, greater than the nearest-neighbor distance (mean = 0.60 ± 0.04 m) on days within that year that hawks did not attack.

In 1982–1983, on days when flocks re-formed after attack, the mean number of birds within a flock after attack was significantly smaller than the number on that day before the attack (Table 3; $P < 0.01$, Wilcoxon matched pairs test). In years of heavy predation, fewer total birds foraged and the number of birds per flock (mean = 43.7 ± 8.0) was significantly smaller than in years of little raptorial predation (mean = 114.3 ± 10.6 during 1976–1978, $P < 0.001$, Mann-Whitney U test). During 1982–1983, there was no significant difference in initial flock size on days when hawks did and did not attack. The likelihood of success of the hawks did not appear to be correlated with flock size. Hawks made successful captures in flocks that ranged from 23 to 64 members, although the rarity of successful captures could mask a trend that would be more apparent with a larger sample size. The difference in flock size between years did not appear to be due to a difference in the resource base. Samples of fish available in the two years revealed no differences in density or species composition. Birds captured as many fish per unit time on days when they were not attacked in 1982–1983 (mean = 0.7 fish/min) as in 1977 (mean = 0.6 fish/min). In birds that resumed foraging on days after flocks were attacked (Table 3), however, foraging rates dropped significantly ($P < 0.01$, two-tailed Wilcoxon matched pairs test) after the attacks. On 45% of the days the hawks attacked, however, no flocks re-formed in the area during the day of the attack. On 33% of the days that flocks re-formed, they were attacked again by hawks.

Switches in habitat use revealing opposing selective factors.—In the winter of 1983, as hawk attacks persisted, the flocks switched to more open habitats (reef and deforested inlets), even when these habitats yielded fewer fish per unit time than did the mangroves, which had abundant fish. This switch was particularly disadvantageous for the herons in terms of foraging efficiency. During the dry season, winds were frequently greater than 20 km/h in the deforested inlets and on the reef, whereas in nearby mangroves they were usually less than 5 km/h. The surface of the water in the mangroves was smooth, due to the wind-buffering effect of the vegetation. In nearby deforested inlets the water was rippled, and herons had difficulty fishing. The mangroves, however, were the favored hunting grounds for the Common Black-Hawks, which used the canopy as cover and as perches from which to launch attacks. In 1982–1983 hawks attacked flocks on 38% of the days the flocks fed in the mangroves, but were never observed attacking flocked herons on the reef or in deforested inlets. Hawks occasionally attacked solitary herons on the reef, but began their attacks farther away than they did in the mangroves and were never observed to be successful in those attempts.

After repeated attacks, individual herons foraged in the mangroves during the rain and at dusk. At these times they caught few fish. Underwater cameras recorded sudden drops in the number of fish available in shallow water as soon as it started raining, and Lythgoe (1979: 96) reviewed studies that showed similar drops in the availability of prey fish at dusk. At dusk crocodiles also became more active. Occasionally, flocks and individuals in 1983 also foraged at midday. At midday many herons gular-fluttered, obviously in distress from the heat, whereas in the morning no herons were observed gular-fluttering. During 1976–1978 herons in this habitat did not forage in the rain, and very rarely foraged at any times other than 0705–1030. In 1982–1983 the Common Black-Hawks were most active from 0800 to 1000, and were never seen hunting in the rain.

Alarms.—I never observed herons giving alarm calls immediately before actual attacks by either hawks or crocodiles. However, alarm calls ("skows" or "skawks") were given when a predator was still at a distance. When this happened, members of the flock first became alert and then took flight if the predator continued to approach. There were also instances when one flock member made a silent, low, swooping U-shaped flight over the flock or over other individuals in the area, and the others

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TABLE 3. Mean (±SE) flock size, foraging rate, nearest-neighbor distance, and proportion of white to total birds within mixed-species heron flocks in years of no raptor predation (1975–1978) and on days when hawks attacked in 1982–1983.

| | | On days hawks attacked | |
	1975–1978	Before attack	After attack
Herons/flock	114 (±10.6)	42.6 (±10.4)	5.9 (±1.8)
Foraging rates (fish/min)	0.60 (±0.05)	0.71 (±0.14)	0.32 (±0.16)
Nearest-neighbor distance (m)	0.33 (±0.01)	0.74 (±0.14)	0.92 (±0.08)
Proportion of white herons[a]	0.76 (±0.05)	0.75 (±0.07)	0.72 (±0.10)

[a] Great Egrets, Snowy Egrets, and immature Little Blue Herons divided by total birds.

immediately took flight. In many of these, a predator, usually a hawk at a distance, was visible, so they are termed "alarm flights." Alarm flights differed from the flights made by birds fleeing a predator. They were lower, slower, and in a curved direction over other birds rather than a straight direction away from the flock. The distribution of these alarm calls and flights among the different-colored herons differed. Dark birds gave alarm calls and made alarm flights significantly more often than white birds (dark birds: 63 calls, 12 flights; white birds: 1 call, 3 flights; $\chi^2 = 202$, $P < 0.001$). Dark birds also tended to occupy more peripheral spots in the flock, so that, on average, they were closer to an approaching predator than other flock members. However, among the most peripheral birds in each flock, a mean of 41% were white. Even when the proportion of white birds at the periphery was used to calculate expected values for white and dark birds, the dark birds gave significantly more alarm calls than would be expected ($\chi^2 = 41.5$, $P < 0.001$). Thus, position alone did not predispose dark birds to give disproportionately more alarm calls than white birds.

DISCUSSION

Predation and conspicuousness.—Predation is an important selective pressure on adult herons, especially in the tropics. It differentially affects white and dark herons. The model experiments demonstrated that white herons attract more hawks than do dark herons in mangrove habitats. In a different habitat (e.g. sandy beaches or open water with glare from the sun), qualitatively different results might have been obtained, but the Common Black-Hawks did not hunt in those habitats. Hawks relied on canopy to make their approach inconspicuous and on perches to launch their attacks. They rarely attacked far from the canopy, and I could not lure them to models out on the reef. Likewise, herons commonly forage along rivers, in marshes, and on mudflats where there is either vegetation or a dark substrate. The experiments were conducted under the conditions where predation is most frequently observed in the Neotropics. My results suggest that morphs that better match their backgrounds from a predator's perspective are at less risk from predation.

Movement and relative advantages of colors.—The experiments in this study involved stationary models, and movement possibly could affect detection by predators. Hawks, but not crocodiles, were attracted to the stationary models. A small number of captive crocodiles (unpubl. data) responded to moving models but not to stationary ones. Even if movement is a predator's major clue to detecting prey, and color vision is minimal, contrast between an object and its background will determine whether that moving object is detected (Lythgoe 1979). Thus, it is unlikely that movement alone would alter relative advantages of white vs. dark plumage in any particular habitat. Furthermore, herons do a great deal of foraging by standing nearly motionless. For these reasons, results with the stationary models in real habitats would be expected to be germane to the predatory situation many herons face.

Experience vs. conspicuousness.—White Little Blue Herons are not only conspicuous but also less experienced than their blue conspecifics. This is unlike the situation in other dimorphic herons. It might be argued that the hawks were attracted by the inexperience rather than by the white color of the immature Little Blue Herons. Inexperience could be reflected by different behavior of white and blue herons, or the prior experience of hawks with white and

blue herons could affect subsequent attraction. However, I think the inexperience of white Little Blue Herons is unlikely to have caused their greater attractiveness in the model experiments. First, the white and blue models did not behave differently, and yet the white models attracted significantly more hawks. Second, Snowy Egrets outnumbered immature Little Blue Herons by 10 to 1. A hawk that approached a random white bird was more likely to find a Snowy Egret than an immature Little Blue Heron, and, hence, to have had experience with a Snowy Egret rather than with an immature Little Blue Heron. The differences in appearance between Snowy Egrets and immature Little Blue Herons are subtle. There is no reason to think that a hawk flying far overhead would discriminate these differences until it was close enough to have been observed in this study. The one time a real Snowy Egret approached the model flock of immature Little Blue Herons, a hawk attacked the Snowy Egret, not the model. There is no reason to think that adult Snowy Egrets are less experienced than adult Little Blue Herons, and there was no evidence that hawks attacked immature Little Blue Herons more frequently than Snowy Egrets foraging under similar circumstances.

Conspicuousness vs. oddity.—I found no tendency for hawks to attack "odd" individuals, as has been suggested (reviewed by Curio 1976: 117–119). Thus, in mixed flocks of herons and egrets, conspicuousness with respect to the background vegetation and substrate appears to be more important than oddity with respect to other group members in eliciting the attacks of predators. This could explain the unchanged diversity of the flocks after predatory attacks and in years of heavy predation. Even though the size of the flocks changed as a result of predation, the composition of the mixed-species flocks remained the same.

Predator detection in mixed flocks.—Solitary-foraging herons ran a greater risk from predation than did herons in flocks, as in other birds (Kenward 1978, Lazarus 1979). This supports the prediction for conspicuous prey (Treisman 1975, Taylor 1979) that the benefits of sharing information about a predator outweigh an increase in detectability. This is important and could explain the prevalence of large heron flocks in the tropics, where large predators are more numerous than in temperate regions.

These flocks are almost always mixed- rather than single-species (Caldwell 1981). One potential advantage of mixed- over single-species flocking is the increased protection afforded by having more varied predator detectors (Altmann and Altmann 1970, Gautier-Hion et al. 1983, Thompson and Barnard 1983). Differences in eye morphology among the species in the flocks could result in differing predator-detecting capabilities (Caldwell 1979). I also showed that there were differences in the likelihood of giving alarm signals. Although theoretical models predict that there will be sentinels on the perimeter (e.g. Treisman 1975), that dark birds should give more alarm calls than white birds in the same relative position is something of an enigma. If there is an advantage to being a dark bird within a flock, as there seems to be, why should the dark birds increase their relative conspicuousness by vocalizing? This might be a result of increased vigilance, as suggested by their lower foraging rates within the flocks (Caldwell 1981); or the more experienced adult Little Blue Herons might be warning their offspring and relatives within the flock, with unrelated flock members benefiting only because of their proximity. The latter explanation, however, would work only if kin tended to flock together. The persistent aggressive attacks of adult Little Blue Herons toward immature conspecifics, attacks that were more violent and prolonged than the attacks that resulted in usurpation of foraging sites (Caldwell 1980), suggest that adults were trying to make offspring disperse, and that kin selection (Sherman 1977) is unlikely to be responsible for the pattern of alarm calls. The pattern cannot be explained by experience alone: adult Snowy and Great egrets were less likely than dark birds to give alarms. A likely alternative explanation would be that the alarms not only warn others within the flock, but also signal to the predator that it has been sighted and has little chance of success (Smythe 1970). The alarm then confers a selective advantage to the alarm sender, as well as to other group members. None of the observed raptor attacks occurred after alarm signals had been given by the herons.

Effects of predators on heron flocks compared with other flocks.—In mixed flocks or in flocks with a dominance hierarchy, some models (e.g. Pulliam 1973) suggest that under predation pres-

sure the subordinate members should progressively disband, because they are more likely to be peripheral and subject to greater risk from predation (Vine 1971, Inglis and Lazarus 1981). In mixed heron flocks, Tricolored and adult Little Blue herons are subordinate to members of other species and tend to hold peripheral positions (Caldwell 1981). Although the flocks diminish in size after predatory attempts and in years of heavy predation, however, it is not through disproportionate loss of members of subordinate species. The proportion of each species and the proportions of light and dark herons in flocks remain remarkably stable. An insight into why peripheral herons might remain with flocks is gained by considering the method of attack of the particular predators involved. The Common Black-Hawk's reliance on canopy to make its approach inconspicuous means that it seldom attacks the most peripheral birds. Crocodiles lie in wait, rather than approaching from outside the group. Thus, the most peripheral herons do not appear to be at a disadvantage in being attacked, although they are probably the ones first seen by an avian predator.

Heron flock size decreases with predatory pressure, unlike the situation in other birds (e.g. Caraco et al. 1980, Myers 1984). It is also contrary to predictions from studies that found decreases in the amount of time an individual spends vigilant with increased flock size (e.g. Powell 1974, Dimond and Lazarus 1974, Lazarus 1979, Caraco et al. 1980, Elgar and Catterall 1981, Elcavage and Caraco 1983) or considerations of the antipredatory dilution effects of groups (Hamilton 1971, Vine 1973). Rubenstein (1978), however, predicted that group size should decrease after a certain point because of diminishing advantages gained by additional sentinels. Several studies have shown that, beyond a certain group size, increases produced no advantages in decreased time spent vigilant (e.g. Berger 1978, Barnard 1980), in probability of detecting a predator (Siegfried and Underhill 1975), or in protection from a predator (e.g. Page and Whitacre 1975, Kenward 1978, Kus 1980). The group size beyond which antipredatory benefits do not accrue can be rather small (30 House Sparrows, *Passer domesticus*; 15 Wood Pigeons, *Columba palumbus*; 5 bighorn sheep, *Ovis canadensis*). Most of the studies that showed antipredatory advantages increasing

with group size dealt only with small flocks. The mean of 114 flock members seen in heron flocks in years with little predation thus could be well over the optimal size for detection of predators. Treisman (1975) suggested that group size should increase with predatory pressure only if flock members do not adjust levels of vigilance. Heron foraging rates decreased after predatory attacks, suggesting that herons adjusted their levels of vigilance. Because herons spend much of their time watching flockmates, and flockmates can provide information about foraging or about predators, it is difficult to measure directly the time they are vigilant for predators.

Distances between neighboring herons in flocks increased with increased predatory pressure, contrary to findings in other birds (e.g. Myers 1984) and to theoretical predictions (Hamilton 1971, Clark and Mangel 1984) of more closely packed aggregations in the presence of predators. Vine (1973), however, pointed out that "spacing out" within flocks presents a fragmented target that is harder to spot and decreases the distance at which the flock can be detected by a predator. A crowded aggregation could interfere with sighting a predator (Treisman 1975) or fleeing from one (Mangel pers. comm.). Whether increased interindividual distance in heron flocks is an adaptation to predatory pressure, or whether it is a result of the disruption caused by the predators, remains to be tested.

Indirect effects of predatory attempts on fitness.—Deaths and possible injuries are not the only fitness-reducing effects of predation. Predatory attempts were associated with decreased foraging rates and with decreased time at foraging sites. After predatory attempts, herons foraged under thermoregulatory stress, in resource-poor habitats, and at times and under climatic conditions that were not conducive to catching fish. Herons under predator-induced stress may not metabolize the fish they ingest as well as if unstressed. A stressed bird may have neither the fat reserves nor the hormonal balance necessary to breed successfully. Migratory birds may be at a disadvantage if they do not garner adequate fat reserves for migration, but residents have to deal with predatory pressures year-round rather than seasonally.

The switches in habitat use by herons under predatory pressure result in poorer foraging and

show two opposing selective factors at work, a rare demonstration in the field. Compromises in foraging, not immediate injury, may be the most important consequence of predatory pressure for most members of many species. In herons, under the conditions prevailing in these mangroves, predation and foraging give selective advantages to two different color morphs. White herons have a foraging advantage (Caldwell in prep.) in the same habitat where they face a greater risk from predators.

Dimorphism in Little Blue Herons.—Predation plays an important role in the balance of advantages and disadvantages associated with color in Little Blue Herons. The immature, rather than the adult, carries the greatest risk resulting from color alone. The immature has the conspicuous white plumage while it is learning to forage effectively (Recher and Recher 1969), and mortality in the first postfledging year is high (74% for white birds. vs. 33% for adults; Dusi 1963). However, the immatures at least partially compensate for these disadvantages by their increased ability to integrate into the largely white mixed flocks (Caldwell 1981), accruing not only the associated foraging advantages, but also the dilution effects of the flock. There is also evidence that white plumage scares away fewer fish than blue plumage in certain habitats (Mock 1981, Caldwell in prep.), whereas in other habitats blue plumage confers foraging advantages (Caldwell in prep.). In addition, the adult has the advantage of inconspicuous blue plumage during times in its life when it would be flying back and forth between foraging grounds and its nest, and conspicuousness to predators would be most disastrous. The change from white to blue plumage could be an important signal to a potential mate that a bird has survived the foraging and predatory rigor of the first year and therefore would be a better provider to potential young. Notably, few white-plumaged subadults mate successfully (Rodgers 1978).

Predation and ardeid color dimorphism.—Ardeid dimorphism is primarily a tropical and subtropical phenomenon (Recher 1972). Among species where only certain populations are dimorphic, the dimorphic populations are restricted to the tropics and subtropics. Little Blue Herons are probably the least tropical of the dimorphic herons, because both morphs can be

found as far north as Massachusetts (Osborn and Custer 1978) during the summer. Previous attempts to correlate ardeid plumage color with temperature or other features of tropical life have been unsuccessful (e.g. Recher 1972, Holyoak 1973). The Ardeidae are of great antiquity (Hancock and Elliott 1978), probably originating at a time when large predators were more plentiful than they are today. I demonstrated that predation on adult herons can be a significant component of daily life in the tropics even now, and that risk from predation varies with color. Predatory pressure is a factor that should not be ignored in considering the evolution and maintenance of color dimorphism in herons.

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