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THE RELATION OF HUNTING SITE CHANGES TO HUNTING SUCCESS IN GREEN HERONS AND GREEN KINGFISHERS

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Considerable information is available on the feeding habits of herons and kingfishers (e.g., Skutch 1957, 1972, Meyerriicks 1960, 1966, 1971, Slud 1964, Jenni 1969, Recher and Recher 1972, Kushlan 1973, Tjornlig 1973). Several authors suggest that herons which hunt by standing and waiting and by wading or walking slowly will eventually move to a new location if no prey approach closely enough to be attacked; however, nothing is said about the tendency to move or stay after an attempt at prey capture. Kingfishers, which hunt from perches and attack more distant prey than do herons, sometimes move to a new location, both after an attempt and when no attempt has been made. To our knowledge, no one has investigated quantitatively the relationship between moving to a new location and hunting success at the previous location, for either herons or kingfishers. Our purpose was to study this relationship in Green Herons (*Butorides striatus*) and Green Kingfishers (*Chloroceryle americana*).

METHODS

We conducted our study at a shallow, 7-acre, artificial lake on the grounds of the Centro Agronomico Tropical de Investigacion y Enseñanza near Turrialba, Costa Rica (9°53'N, 83°38'W), at an altitude of 700 m. It is near the lower limit of the premontane wet forest life zone (Tosi 1969). The east shore and most of the north shore of the pond are overgrown by dense stands of papyrus (*Cyperus papyrus*). A small island containing several small clumps of bamboo (*Bambusa* sp.) is located in one corner. Water lilies (*Nymphaea* spp.) and floating mats of aquatic fern (*Salvinia auriculata*) interspersed with small patches of open water and mud islands cover about 80% of the surface. The rest is covered by emergent vegetation up to 1 m high. The vegetation was described in detail by Jenni and Collier (1972). Approximately 15 bamboo poles, projecting 0.5-2 m above the surface, are scattered throughout the lake.

Between 29 March and 26 June 1974 we watched two individually identifiable (one was banded; one had a misshaped foot), but unsexed, adult Green

Herons for about 15 h each. Observation periods ranged from 3 to 102 min ($\bar{X} = 73$ min, $N = 25$ sessions). Between 5 October and 12 December 1974 we watched adult Green Kingfishers for 12 h. During this period we saw only one male and one female at the same time, and we assumed that all our observations were of the same male (9 h) and female (3 h). Observation periods ranged from 5 to 78 min ($\bar{X} = 22$ min, $N = 32$ sessions). Additionally, we casually observed both species throughout 1974; these observations showed that species differences discussed below existed throughout the year and were not a product of the different times of data collection.

We noted when the observed bird changed locations or attempted to catch prey and we recorded the time to the nearest 5 s. We also recorded whether attacks were successful. For each location change, we calculated either the period of time an individual spent at a location before and after an attack or the period of time it remained at a location without attacking. The time a heron spent eating was deducted from the total time spent at the location where it ate. Eating time was always less than 5 s for the kingfishers and was not recorded.

RESULTS

We combined the data for both individuals of each species because we found no significant individual differences for any of the parameters measured (Mann-Whitney U tests). The herons hunted mostly from the small mud islands and from rocks along the shore and infrequently from the bamboo poles, emergent vegetation and sides of a small skiff. They used the standing-and-waiting technique almost exclusively during our observations, but occasionally walked slowly along the shore. Herons always took prey less than 1 m away. The kingfishers hunted primarily from the bamboo poles, papyrus, and the bamboo trees on the island, and occasionally also from the emergent vegetation and rocks. Most of these perches were 1-2 m above the water but ranged from 0.3-5 m. We also saw kingfishers make several attempts after hovering 4-6 m above the water's surface. Both the heights of the perches and the hovering differ from Slud's (1964) report that these birds dive from low perches and not from hovers. Kingfishers took prey up to 6 m away. The minimum distance between locations was approximately 4-5 m for herons and 2-3 m for kingfishers; both species flew between locations.

The median lengths and ranges of times spent at locations are listed for the two species in Table 1. Three aborted attempts by kingfishers, in which the bird dove toward, but did not enter the water, are included as unsuccessful attempts. The ranges in

TABLE 1. Median length and range of time (min:s) spent at a location.

	Green Herons			Green Kingfishers		
	N	Median	Range	N	Median	Range
When no attempt is made	273	1:10	0:03-30:05	40	1:23	0:03-16:21
Prior to an attempt	73	2:50	0:02-21:49	70	1:21	0:05-10:29
After an attempt	73	0:35	0:02-40:59	38	0:46	0:08- 5:28
Successful	39	0:54	0:04-15:03	19	0:59	0:24- 5:13
Unsuccessful	34	0:11	0:02-40:59	19	0:57	0:08- 5:28

Table 1 overlap considerably due to a few very large numbers and all of the distributions are skewed to the left. The distributions were compared with the Mann-Whitney U test because it is sensitive to differences in central tendency without being affected greatly by a few extreme observations.

Herons spent significantly more time at a location before an attack than when they moved without having made any attack ($U = 7669.5$, $z = 3.48$, $P < 0.0003$). Also, herons moved to a new location much sooner after an attack than when no attack was made ($U = 14,360$, $z = 4.79$, $P < 0.00003$). Of observations when attempts were made, herons stayed at a location significantly longer after a successful attempt than after an unsuccessful attempt ($U = 310.5$, $z = 2.52$, $P = 0.006$). There were no significant differences in similar comparisons for the kingfishers.

A comparison of the two species showed that herons spent more time at a location before an attack ($U = 1906.5$, $z = 2.95$, $P = 0.003$) and less time in a location after an unsuccessful attack ($U = 417$, $z = 2.58$, $P = 0.01$) than did kingfishers. There was no significant difference between the two species in the time spent after a successful attempt ($U = 412$, $z = 0.69$, $P = 0.49$).

Eighty-five of 96 (85.4%) attacks made by herons were followed by a location change prior to the next attempt, compared to only 90 of 179 (50.3%) attacks made by kingfishers (Table 2); this difference between the two species is statistically significant ($\chi^2 = 22.6$, $P < 0.001$). The average number of consecutive attempts at a location was 1.1 for herons and 1.8 for kingfishers. The greater tendency for kingfishers to make successive attacks from a location also is demonstrated by comparing the distributions in Table 2 with Poisson distributions. The distribution for the kingfishers is clumped ($\chi^2 = 13.8$, $P < 0.05$) while the distribution for the herons does not differ significantly from random ($\chi^2 = 1.6$, $P < 0.5$).

DISCUSSION

The differences observed between Green Herons and Green Kingfishers in their tendency to move to a new hunting location may be related to differences in hunting strategy and attack radius. Herons stand and wait for prey to approach and have a small attack radius. Kingfishers fly to their prey and their much larger attack radius may approach the maximum distance at which they can visually detect prey. Why do herons, but not kingfishers, remain longer at a location before an attempt than when no attempt is made? First, herons probably remain longer if watching a prey item that is out of reach than if no prey are visible. Second, continuing to wait at one location should result in some prey animal eventually approaching close enough for an attempt. Not having

to wait for prey to approach, kingfishers can attack as soon as an item is seen and can change locations when no prey are visible from that site.

Why do herons remain longer than kingfishers at a location before an attempt? In addition to their hunting method, changing locations probably takes more energy for herons. They launch their large bodies into flight from a position near water level while kingfishers simply dart from perches. Third, the fish taken by kingfishers may be more clumped than the frogs and tadpoles taken by herons. It may then be profitable for the kingfishers to change perches quickly until a school is located. Fourth, fish may be more abundant than frogs and tadpoles, resulting in kingfishers sighting prey sooner than herons after arriving at a location. We did not measure abundance of prey, but tadpoles, frogs, and fish all seemed plentiful, making this explanation the least likely.

Herons change locations more often after attempts than do kingfishers. This may be because attacks generally disturb the water throughout the small area hunted by a heron. If this frightens the rest of the prey out of the hunting area or causes them to hide, it probably is more profitable for a heron to move to a new location than to wait until prey again appear in the area of the previous attack. A kingfisher's attack usually produces a larger splash than a heron's thrust, but the waves and probably the sound are quickly dampened by vegetation. Also, kingfishers minimize their silhouette by usually attacking from low perches and by flying low over the water, then rising abruptly to the perch when returning from an attack or when changing perches. Thus, attacks by kingfishers do not disturb the water and probably do not frighten prey throughout their large hunting area. Moving to a new location after an attempt, regardless of success, may not be more profitable than continued hunting at the old location, at least as long as prey are visible occasionally.

Although herons usually move soon after an attempt, they stay longer after a successful attempt than after an unsuccessful one. First, a successful attempt may provide positive reinforcement for hunting at

TABLE 2. Number of times one or more attempts were made from one location.

Species	Number of attempts at one location							Total number of attempts	
	0	1	2	3	4	5	6		7
Green Herons	273	70	11	0	1	0	0	0	96
Green Kingfishers	40	45	21	13	6	3	0	2	179

that location. Second, observed eating times were as long as 83 s and it is possible that by the time the heron finishes eating, prey occasionally are visible again in the same area; however we found no correlation between eating time and whether or not a heron moved. Third, variations in hunting motivation may influence the tendency to remain; after eating, a heron should be less hungry and thus may be less motivated to change location.

SUMMARY

The relationship between tendency to move to a new location and hunting success at the previous location was quantitatively investigated in Green Herons (*Butorides striatus*) and Green Kingfishers (*Chloroceryle americana*). Herons stayed in one location longer before a prey-catching attempt than when no attempt was made, moved sooner after an attempt than when no attempt was made, and stayed longer after a successful attempt than after an unsuccessful attempt. There were no significant differences in similar comparisons for the kingfishers. Herons stayed in one location longer before an attempt and moved sooner after an unsuccessful attempt than did kingfishers. Kingfishers made consecutive attempts from a location more often than herons and more often than predicted by chance. Explanations for these habits are suggested.

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WEATHER-DEPENDENT FORAGING BEHAVIOR OF SOME BIRDS WINTERING IN A DECIDUOUS WOODLAND: HORIZONTAL ADJUSTMENTS

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Although avian feeding niches have been heavily studied, the influence of short-term weather variation on foraging has received scant attention. I have shown previously that birds wintering in a temperate deciduous woodland in New Jersey significantly modified several aspects of their foraging behavior in response to changing wind velocity and temperature (Grubb 1975). The birds positioned themselves closer to the ground in lower temperatures and higher winds, most likely to reduce thermal stress by moving into the area with reduced air movement near the forest floor. Such descent then significantly modified the choices available to the bird of substrate type and tree species for foraging.

The New Jersey study plot was selected in part to eliminate any complicating horizontal adjustments by the birds. Local topographical variation was negligible, and habitat edges were absent. The present

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study, in a different woodland, tests the predictions that decreased solar radiation, higher wind velocities, and lower temperatures in winter cause foraging birds to decrease their exposure to wind by: (1) capitalizing on topographical variation; and (2) using leeward sides of foraging substrates. Each weather variable is examined separately by grouping sightings so as to hold the other variables constant or within narrow ranges.

METHODS

From November to March 1973-75, I watched birds foraging in a 26-ha beech-maple woodlot in Bennington Township, Morrow Co., Ohio. The woodlot is rectangular, with its longer sides oriented north-south, and has a 15-m wide stream valley running its length. A 2-m wide stream meanders through the valley. Thus, the woodlot may be divided into an "east bluff" and "west bluff"; the intervening "stream valley" is separated from the bluffs by 45° slopes 5 to 15 m high. The woodlot is bordered on the north by a road, on the east by a dense old-field thicket of blackberry and hawthorne, and on the south and west by tilled fields (of winter wheat during the study).

Field methods largely duplicated those of Grubb (1975). I watched only the four most abundant species: Downy Woodpeckers (*Picoides pubescens*, ≥