TERRITORY SIZE IN *MEGACERYLE ALCYON* ALONG A STREAM HABITAT

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ABSTRACT.—Belted Kingfishers (*Megaceryle alcyon*) defend both breeding and nonbreeding territories. The small nonbreeding territories serve as feeding territories, and their size is inversely correlated to food abundance. In the breeding season, when nest sites are a limiting resource, territory size does not significantly correlate with food abundance. The average weight of fledglings/nest, however, is significantly correlated with territory size. In both seasons, kingfishers appear to use stream riffles as preferred foraging sites, although pools are more prevalent. Riffles may represent environmental cues by which individuals assess habitat quality. *Received 19 February 1981, accepted 30 September 1981.*

NUMEROUS studies have revealed correlations between territory size and various environmental parameters. Most frequently, resource density (Pitelka et al. 1955, Stenger 1958, Gill and Wolf 1975, Salomonson and Balda 1977) and/or population density (Myers et al. 1979, 1980; Ewald et al. 1980) are cited, but, as is now becoming evident, the proximate causal mechanisms responsible for these correlations are not always obvious. For example, although a negative correlation between territory size and food density may imply that an animal has the ability to assess resource density in relation to its needs, it may actually only reflect the increased population pressure in areas that attract many animals because of high food density. Alternatively, negative correlations might result from an animal's recognition of habitat factors that are directly associated with food (Hildén 1965, Morse 1976) rather than its assessment of food itself. Seastedt and Maclean (1979) have shown that the size of breeding territories of Lapland Longspurs (*Calcarius lapponicus*) is inversely related to the "expected" food density of the habitat comprised by the territory rather than to the actual food density in a given year. They conclude that longspurs respond to the habitat composition of an area rather than to the food density.

The relative importance of different environmental parameters as determinants of territory size may be dependent upon the type of territory defended [see Nice (1941) for classification of territories]. For example, breeding territories of birds usually possess multiple resources, such as nest sites and food, while non-breeding territories are often only "feeding territories" (Welty 1975); thus, in the breeding season, the number and distribution of available nest sites may influence the suitability of a habitat (von Haartman 1959). If nest-site limitations restrict the total number of breeding birds, territory sizes may become less dependent upon the availability of other resources such as food.

Belted Kingfishers (*Megaceryle alcyon*) are overtly aggressive birds that, along small streams, defend territories with well-defined boundaries and maintain exclusive use of the resources on their territories. Although the strong territorial nature of this bird is well known to naturalists, I am unaware of any previous empirical studies reporting analyses of the territoriality of this species. During the breeding season (March–June), both the male and female of a breeding pair jointly defend the territory on which their nest is located. Nest sites are chosen before the boundaries of breeding territories are firmly established (Davis 1980). In the autumn, birds of both sexes, including the young of the year, defend individual territories. The present study investigates possible determinants of territory size in the Belted Kingfisher in both the breeding and nonbreeding seasons.

STUDY AREA AND METHODS

Kingfishers were observed along a 16.8-km stretch of Indian Creek in rural southwestern Ohio. During

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the study period, Indian Creek had an average flow rate of 1.9 ± 0.4 m^3/s, although runoff produced from heavy rains occasionally increased the volume of flow (at times by as much as 10×). Creek width and depth varied from 5 to 19 m and 0.05 to 1.8 m, respectively, at normal flow. Turbidity was usually low except after heavy rains. Substrate varied; loose rock was predominant in riffles, while gravel and sand were the usual substrate of deeper pools. Nesting banks suitable to *M. alcyon* occur regularly along Indian Creek where the water erodes soil from bordering banks. Secondary forest growth dominates much of the creekline. Dominant tree species are American sycamore (*Plantanus occidentalis*), sand bar willow (*Salix interior*), several maple species (*Acer* spp.), and a variety of oaks (*Quercus* spp.).

The bulk of the data was collected between January 1978 and October 1979. Kingfishers were banded with U.S. Fish and Wildlife bands and marked with lead-free paint along the edge of the rectrices, using a combination of four colors. Individual birds could easily be identified in the field within a 50-m range using binoculars.

The territory size of marked individuals was measured as length (m) instead of as area, because territories followed the course of the stream. Territory sizes were assessed by recording the movement of marked individuals that were "herded" along their territories (Wiens 1969). By walking along the stream, I forced the resident kingfisher(s) to fly ahead until the end of the territory was reached. At this point the kingfisher(s) would reverse direction to fly back into its territory. The locations of the up- and downstream boundaries were determined a minimum of five times by this method. The site of aggressive confrontation between adjacent territory holders was used to confirm boundaries between territories. Lateral boundaries of territories were demarcated by the treeline along the edge of the stream. The following information was later transferred to detailed maps: length and width of stream, depth measurements of stream, lengths of pools and riffles, lengths of exposed banks, location of nests, and number of perches along the stream's borders. Riffles were defined as turbulent flow (5–15 cm in depth) connecting pools. Six nonbreeding territories were measured in the fall of 1978, 11 breeding territories in the spring of 1979, and 21 nonbreeding territories in the late summer and fall of 1979.

Two methods were used to determine the size and species of prey selected by *Megaceryle alcyon*. In the first (24 May–23 June), I assessed the species and size of prey brought to the nest by observing adult feeding activity with the aid of blinds and a 20× telescope. Because kingfishers carry prey in their beaks, I could estimate fish size by comparing the length of the fish with the bird's bill (culmen length of individual birds was recorded during banding; Drent 1965). Prey were classified to family, genus, or species by noting the morphological characteristics of the respective taxonomic groups. Cyprinids were classified into one of three groups: stonerollers (*Campostoma anomalum*); minnows, which included all identifiable cyprinid species other than *C. anomalum*, or unidentified cyprinids, which included all specimens that could not be identified to genus. The second method (1 June–23 June) involved placing velcro collars around the necks of nestling kingfishers for a period of 2 h from 0700 to 0900. This procedure prevented the young birds from swallowing food brought to them by the adults, and, as a result, fish accumulated at the entrance of the nest chamber. Weight, length, and species of these fish were recorded. Additional data on prey size and type were collected as kingfishers were observed fishing or when items were dropped into the mist net during banding of adults.

Estimates of food abundance were obtained for six nonbreeding territories (September–October 1978) and for six breeding territories (June 1979) by sampling the entire length of each territory by electroshocking. A shortage of manpower prevented fish sampling on any of the 21 nonbreeding territories measured in 1979, but in October 1979, 1,200 m of Indian Creek were electroshocked, with pools and riffles sampled separately, in order to document the relative location of the different fish species. Electroshocking was accomplished by suspending two electrodes, positioned at opposite ends of 1.3-m pole, in the water while moving upstream at a constant speed. Current was supplied to the electrodes by a 110-volt AC (1,500 watt) generator. Shocked fish were collected in nets by two persons following a third person carrying the electrodes. Fish collected were counted and classified according to size and species before they were returned to the stream. Fish mortality was reduced to less than 1% by supplying oxygen to the collecting buckets via air-stone and portable air pump.

Electroshocking was the method of choice for several reasons: (1) it was more practical for sampling long stretches of streams (seining was the alternative method); (2) sampling of only surface fish was desired; and (3) although small fish are generally less sensitive to sampling by this method than larger fish, the size of fish vulnerable to predation by kingfishers (4–14 cm) appears easily sampled by electroshocking (McCormack 1962; results of preliminary sampling by the author). Fish were assigned into five size classes: 4–5.9 cm, 6–7.9 cm, 8–9.9 cm, 10–11.9 cm, and 12–14 cm. Fish smaller than 4 cm and larger than 14 cm were excluded from the samples, as these extreme sizes were never seen taken by kingfishers.

For each fish species, 15 specimens in each size class were weighed to obtain an average weight for that size class. These averaged weights were multi-

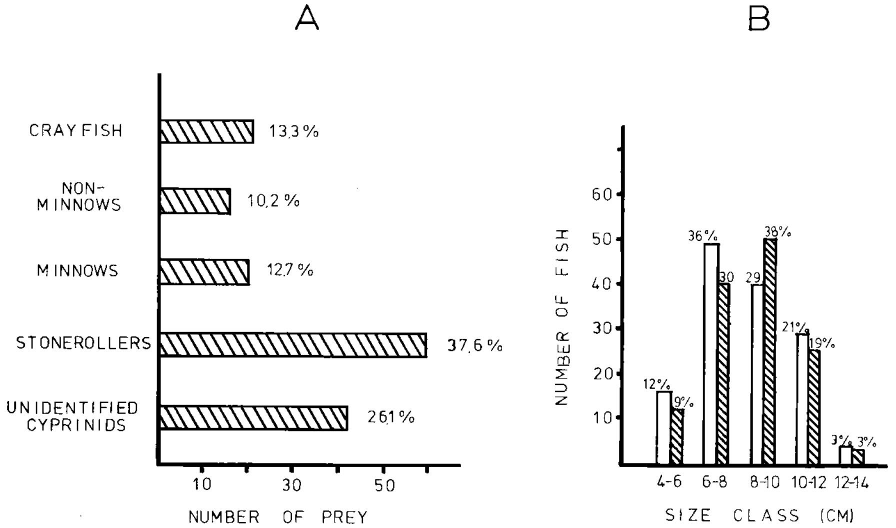

Fig. 1. Food capture data. Shown are the species composition (graph A) and size (graph B, hatched bars) of prey items taken by kingfishers. Data are from observations made on 22 dates and from velcro collar method (see text for details). Open bars in graph B represent the expected number of fish in each size class that should be taken by kingfishers, calculated from the percentage of each size class present in electroshocking data (breeding season 1979, total number of fish sampled = 3,678).

plied by the number of individuals sampled within each size class; then, all size classes were added together to obtain the total grams of fish per species. The number of grams of each species were added together and divided by the length of stream sampled to obtain the total grams per meter of stream. Relative food abundance per territory was calculated from these data (grams$\cdot$meter$^{-1}\cdot$territory^{-1}).

Preferred foraging sites of individual birds were identified. Each time a bird was observed foraging, selected stream parameters of the immediate habitat were recorded, e.g. whether the individual was seen fishing in a shallow pool (depth < 30 cm), a riffle (as previously defined), or deep pool (depth > 30 cm). Both sexes were included, and data were collected on 15 separate dates during the fall of 1979.

Between April and June 1979, data were collected from 14 nests on Indian Creek. Recorded were: (1) number of eggs laid, (2) number of eggs hatched, (3) weight of nestlings (g), (4) incubation period (days), and (5) number of young fledged. To sample each nest, I dug an entrance from the top of the bank down to the backside of the next chamber. A pre-cut plywood door assembly was used to reseal the nest chamber between visits. Nests were checked an average of once a week; near fledging, nests were checked every other day. Data collection is more likely to cause nest desertion early in the nesting cycle (i.e. before incubation) than after the eggs have hatched. In very early spring (1979), two nests were deserted, but in each case new, successful nests were made within the original territory.

RESULTS

Prey and foraging behavior.—Cyprinid species comprise the majority of the kingfisher's diet (Fig. 1A); stonerollers (*C. anomalum*) were observed most frequently. If, as suspected, a substantial proportion of the unidentified cyprinids in Fig. 1A are *C. anomalum*, this species would be under-represented in the figure. In addition, the percentage of crayfish (*Cambarus* spp.) may not reflect the importance of this species; 19 of the 21 observations of kingfishers bringing crayfish to the nest occurred during periods of high water and high turbidity when fish were difficult to catch.

The size range of fish taken by kingfishers is shown in Fig. 1B. Also shown is the "expected" distribution of prey, calculated from the proportion of each size class represented in the electroshocking data from Indian Creek (data are pooled from all territories). A Chi-square test showed no difference between the observed and expected sizes taken ($\chi^2 = 5.08$; $0.3 > P > 0.2$; df = 4), indicating that kingfishers take prey of different sizes in propor-

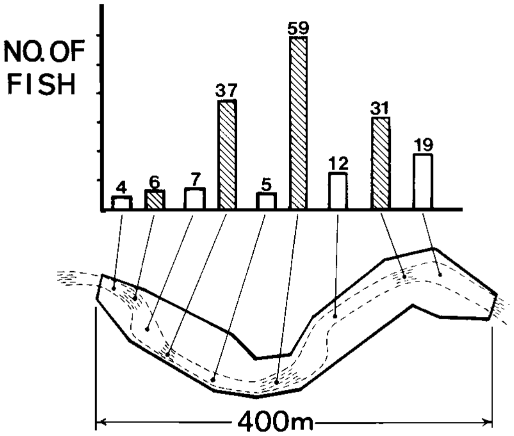

Fig. 2. Distribution of fish in pools and riffles of a typical nonbreeding territory. Hatched bars represent numbers of fish caught in riffle sections; open bars represent numbers of fish caught in pools.

tion to the relative abundance of each size. Appropriate data are not available to test adequately whether or not kingfishers select increasingly larger prey across the nesting season to feed their progressively larger young. The size distribution of the fish electroshocked in the nonbreeding season suggests that small fish are more abundant than would be predicted from the spring data ($\chi^2 = 79$, $P \gg 0.01$). It is unknown whether or not kingfishers take on-the-average smaller prey in the non-breeding season, but field observation confirms that they continue to feed mainly on fish (Davis 1980).

In both seasons, stonerollers are the most abundant prey species, comprising 70% of the total fish sampled by electroshocking in the nonbreeding season (data pooled from 1978 and 1979) and 72% in the breeding season; cyprinids other than stonerollers comprise 20% and 21%, respectively. There is no statistical difference in the proportion of stonerollers to "minnows" between seasons ($\chi^2 = 0.109$, $P > 0.7$, df = 1; total fish sampled in the nonbreeding season = 3,578, in the breeding season = 3,678), although noncyprinid species are more abundant in the non-breeding season ($\chi^2 = 32.68$, $P < 0.001$, df = 1). This relatively large proportion of stonerollers explains the large proportion of this species in the kingfisher's diet (Fig. 1A). Eipper (1956) also reports that stonerollers are a favorite prey of kingfishers.

During the initial electroshocking runs, the data from riffles and pools were combined. Although it was evident in the field that significantly more fish were taken from riffles, the initial data could not be analyzed to determine the difference in the number of fish occurring between these areas. Such data were available, however, for the 1,200 m of Indian Creek electroshocked in October 1979. Using these data, the distribution of prey species (fish) was found to be significantly greater in riffles than in pools ($n_{pool} = 12$, $\bar{x}_p = 48.65$ g/m; $n_{riffles} = 12$, $\bar{x}_r = 195.46$ g/m; $t = -3.11$, $P < 0.01$, df = 22; see example in Fig. 2). Stonerollers were most commonly found in the riffles ($\chi^2 = 234$, $P \ll 0.001$, df = 1), while other cyprinids, taken as a group, showed no preference for riffles or pools ($\chi^2 = 1.29$, $P > 0.2$, df = 1). *Campostoma anomalum* is known to be a riffle species (McClane 1978).

In the nonbreeding season, kingfishers use stream habitats differentially: during 80 observations, kingfishers were found fishing long riffles 71.3% of the time, along shallow pools 20% of the time, and at deep pools 8.7% of the time, despite the fact that riffles comprised only 36% of the stream's length ($\chi^2 = 35$, $P < 0.001$, df = 2). Unfortunately, foraging data were not collected for the breeding season, but my observations indicate that kingfishers behave similarly in the spring. Moreover, the predominant use of *C. anomalum* as food in the breeding season suggests that they fish primarily along riffles.

Territories.—Territories defended in the 1979 breeding season were more than twice as large as those defended in the 1979 nonbreeding season (breeding, $n = 6$, $\bar{x} = 1{,}030 \pm 219$ m; nonbreeding, $n = 21$, $\bar{x} = 389.29 \pm 92.63$; $t = 3.55$, $P \ll 0.005$, df = 31). The data are inconclusive as to whether or not food is a causal factor affecting territory size. For example, the size of nonbreeding territories is significantly inversely related to food density (g/m; $r^2 = -0.98$, $n = 6$, $P < 0.01$), while the size of breeding territories is not significantly correlated ($r = -0.71$, $n = 6$, $P > 0.05$). Care must be exercised when interpreting causal relationships from simple correlations: in both seasons, the negative correlations may result from the indirect effect of intruder pressure, i.e. more birds are attracted to higher food densities (Myers et al. 1980).

As mentioned previously, riffles contain significantly more fish than do pools, and kingfishers forage more often at riffles. If riffles are

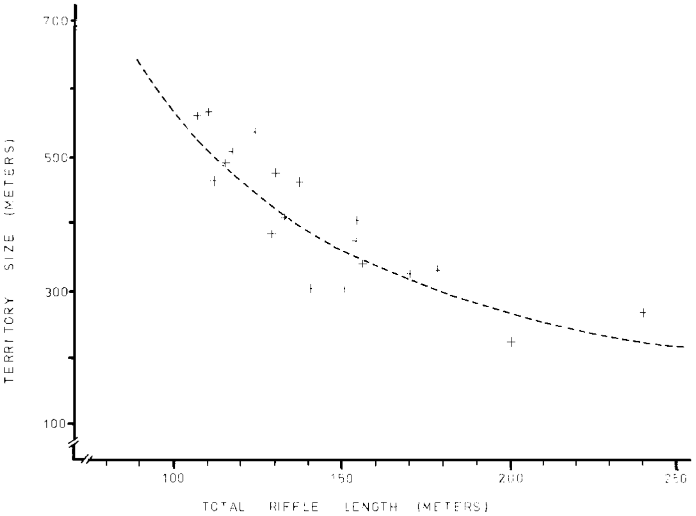

Fig. 3. Riffle length versus size of nonbreeding territories on Indian Creek, 1978. Riffle length and territory size are measured in meters. Data points fit an exponential equation (represented by the dashed line) with $r^2 = 0.75$, $n = 19$ and $P < 0.01$.

an important cue, one would expect territory size to be inversely related to total riffle length, as is the case (shown in Fig. 3) for nonbreeding territories ($n = 19$, $r^2 = 0.75$, $P < 0.01$). Although riffle length and breeding territory size are not significantly correlated ($n = 8$, $r = -0.45$, $P > 0.10$), breeding territories that have a greater concentration of riffles around the nest are significantly smaller than other territories, as is shown in Fig. 4 ($\bar{x} = 827.5$, $n = 4$; $\bar{x} = 1{,}213.75$, $n = 4$; $t = -3.76$, $P < 0.01$, df $= 6$). These results might be explained by postulating different functions for breeding and nonbreeding territories: nonbreeding territories appear to be essentially feeding territories, while breeding territories contain two important resources, food and a suitable nest site.

Nest-site limitation and reproductive success.—Suitable nesting banks appear to be in short supply. Of 24 banks along a 10.6-km section of Indian Creek, 13 banks were occupied by nesting pairs, 6 banks were unsuitable for occupation due to substrate characteristics (composed of a high percentage of clay and/or stone) or location near areas receiving much use by humans (e.g. dredging operations), and 5 banks remained unoccupied due to competitive exclusion by territorial individuals. Belted Kingfishers are not colonial nesters and will defend unoccupied nesting banks from conspecifics if they are within their territories. Starting in March, confrontations between males along sections of streams containing nesting banks were a common sight, suggesting the presence of more males than nesting banks. In addition, females seemed in surplus as well, because, on two occasions when the female of a pair disappeared, a new female took her place with the resident male. White (1953) and Hamas (1974) also reported nest-site limitations for the Belted Kingfisher. An estimate of the number of kingfishers competing for nests is not available due to the fact that birds were not banded until after territories were established.

Relationships of territory size and food abundance with reproductive success are summarized in Table 1. Significant correlations occur between the following sets of parameters: (1) territory size vs. average weight of fledglings ($r = 0.93$), and (2) food density (g/m) vs. number of birds fledged/nest ($r = 0.96$). The fact that food density (g/m) is significantly correlated with number of fledged/nest while territory size is not ($r = -0.45$) suggests that the size of the territory is less important than food density for production of offspring.

DISCUSSION

Nest sites, food, and territory size.—Both the scarcity and location of nest sites in relation to riffles appear to influence territory establish-

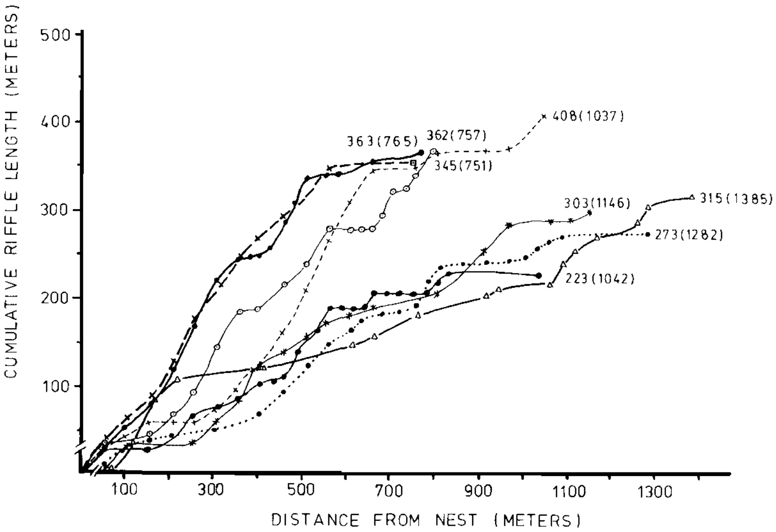

Fig. 4. Cumulative riffle length versus distance from nest. On the ordinate is the cumulative length of shallow water (depth ≤ 15 cm) as the distance from the nest increases symmetrically by 25 m on the abscissa. Data were obtained from detailed maps made of each territory, which included location and length of riffles and pools along the stream. Adjacent numbers represent total length of shallow water (primarily riffles), and numbers in parentheses represent lengths of territories.

ment by *Megaceryle alcyon*. Theoretically, nest-site limitations can suppress the breeding population density and thus lead to a lower level of competition for food than would occur if all potential breeders were able to nest. A scarcity of nest sites is often observed for birds (see Temple 1977), and field observations indicate competition for available nesting sites for kingfishers (Davis 1980). Accordingly, territoriality in the breeding season may primarily serve to secure a nest site, while the need to defend a food resource is secondary. This study presents data that support this hypothesis because territory size and food abundance (g/m) are not significantly correlated.

Other data, however, suggest that food distribution does influence the size of breeding territories, in that territory size appears to be established in a consistent relation to the proximity of productive food patches near the nest (Fig. 4), i.e. the smallest territories enclose the richest food sources. Hole-nesters typically select a nest site before establishing their territories (von Haartman 1957)—a generalization that accurately describes the Belted Kingfisher (Bent 1940, Davis 1980). Unless kingfishers evaluate food abundance during nest-site selection, my data imply that an element of chance enters into the equation that determines whether or not a particular pair of kingfishers will defend a large or small territory. Evidence is not in favor of a random selection of nest sites, however. First, males arrive at least a month before the females to find a suitable nesting bank (some males in mild winters remain the year around). Second, within most breeding territories along Indian Creek, more than one suitable nesting bank was available from which to choose.

In the event that food is concentrated near a nest site, defense of a small territory may save a pair time and energy both in defense of the territory and in the transport of fish back to the nest. To feed a nest full of young kingfishers may require considerable time and energy. Using data from Vessel (1978), I calculate that at maximum growth rate each nestling can consume approximately 11.2 fish/day. Given 15 h of daylight, each adult of a pair would need to catch 2.6 fish/h in order to feed seven young, not including fish for themselves. During unfavorable weather, this may be a difficult task, one that is aggravated if food is located far from the nests. As a result, access to an uncontested and rich food source may be critical for raising a full clutch of young kingfishers. As Seastedt and Maclean (1979) have pointed out for Lapland Longspurs, habitat quality may be better

TABLE 1. A summary of correlations (r) and significance levels between reproductive parameters, territory size, and food abundance. Sample size (n) varies due to the facts that not all territories were sampled for food or nest data were incomplete for some territories.

	Territory size			Food abundance					
				Grams/meter			Total grams		
	r	n	P	r	n	P	r	n	P
Number fledged/nest	−0.45	8	NS[a]	0.96	5	0.02	−0.27	5	NS
Average weight of fledglings per nest	0.93	7	<0.01	−0.50	5	NS	0.62	7	NS
Total weight of fledglings per nest	−0.22	7	NS	0.76	5	NS	−0.39	5	NS

[a] NS = $P > 0.05$.

represented by food density than by total quantity.

When food is not concentrated near the nest, it might be advantageous to defend as large a territory as possible, first, because larger territories may contain greater amounts of food (total biomass/territory) and, second, because larger territories may contain a more reliable food supply, i.e. a larger supply of alternative food resources. During fluctuations in water levels following heavy or prolonged rains, fishing becomes difficult, and kingfishers are obligated to switch to crayfish as prey, a food item not found in riffles. Perhaps as a consequence of both these factors, parents with larger territories that fledge the same number of offspring as those with smaller territories may produce heavier young. These increased fat reserves could increase the chances of survival of fledglings (Lack 1966), because the first few weeks after leaving the nest is a most critical period for young kingfishers. Early attempts at fishing are most often failures for the young birds, because they are weak flyers and apparently must learn how to fish (Bent 1940, White 1953, Davis 1980); the fact that parents continue to feed fledglings suggests that young have difficulty in obtaining their own food. Because *Megaceryle alcyon* typically raises only one clutch per year, the survival of fledglings may markedly affect the relative fitness of breeding pairs. It appears that assessing the relative value of large versus small territories in terms of reproductive success may depend upon environmental circumstances. As argued above, the weight at fledging may be important when the environment fluctuates, but fledging more but lighter young may increase fitness in a more constant, productive environment. Both strategies may be utilized by kingfishers, but the question of why kingfishers defend the sizes of territory that they do is still not answered.

There are two prevailing hypotheses that address the causal relationship between food abundance and territory size (Myers et al. 1980). The first is the "sufficient resource" hypothesis (see Verner 1977), which is derived from the classical concept that the basic function of territoriality is to secure adequate resources. This hypothesis states that individuals should defend only those resources that are required. The second hypothesis predicts that competition is most severe in areas of high resource density, leading to increased costs of defense; as a result, territory size is limited by competition for resources (Seastedt and MacLean 1979; Myers et al. 1979, 1980). Relevant data on the Belted Kingfisher are not yet available to enable a choice between these hypotheses; circumstantial evidence, however, favors the latter. Expansion of breeding territories was observed twice, once in 1978 (Davis 1980) and once in 1979, after an adjacent pair of kingfishers deserted their territory due to human interference at their nests. These observations support the hypothesis that breeding territory size is limited by competition. In a reverse sense, severe nest-site limitations may promote large breeding territories by reducing competition.

In the nonbreeding season, territories of individuals were remarkably constant in size. During prolonged rains, nonbreeding territories were often deserted but were reestablished by the original owners with the original boundaries when the water levels returned to normal. In December, some territories gradually increased in size as kingfishers began to disappear, presumably due to their migration south. When and how many birds migrated appeared to be related to the severity of the weather. During cold periods, accumulation of ice along the stream blocked access to fishing areas; the few birds remaining during the winter months (December–February) seemed to use crayfish more extensively, as gauged by the accumulation of their exoskeletons in the winter roosting nests examined. How dependent kingfishers are on crayfish in the winter is still unknown. Accumulation of exoskeletons may only indicate that these parts are not digestible while most parts of fish are digestible (White 1953). In terms of the proportion of digestible biomass/prey item, fish are probably a higher quality food item.

Proximate cues to assess resource abundance.—Although fish availability may fluctuate during the season (Davis 1980), particular habitat parameters associated with food may remain relatively constant, e.g. the amount of riffles present along a section of stream. Thus, if direct assessment of food by kingfishers is difficult, *Megaceryle alcyon* may instead respond to habitat parameters such as riffles. Morse (1976) believes that warbler species respond to cues that are easily monitored and are correlated to important factors. Similarly, data on Sparrowhawks (*Accipiter nisus*) (Newton et al. 1977) and Lapland Longspurs (Seastedt and Maclean 1979) indicate that these species respond to alternative habitat parameters rather than assessing food density directly. Other species are known to search for specific prey types by searching for specific sites or patches, rather than the prey item itself (Royama 1970, *Parus major*; Alcock 1973, *Agelaius phoeniceus*; Tinbergen 1976, *Sturnus vulgaris*). The Little Green Kingfisher (*Chloroceryle americana*) also prefers to fish along riffles within a stream habitat. Out of 62 observations made by the author in Costa Rica during the summer of 1981, the Green Kingfisher was found foraging along riffles 84% of the time. Kingfishers may not innately recognize riffles but instead learn to associate them with food by positive reinforcement subsequent to fishing success along riffles. Future experiments that manipulate food abundance are needed to determine the role of habitat parameters (riffles) in the assessment of habitat quality.

The general pattern displayed in Fig. 4 suggests that in addition to choosing a suitable nest site, breeding birds are able to use habitat cues as important parameters in establishing territory size. Only one pair defended a territory larger than expected, when size was predicted by the criterion of the cumulative length of riffles. This pair initially defended a smaller territory (approximately 830 m) but increased its size after the adjacent downstream territory was deserted due to human interference at the nest. In addition, the relationship between the size of nonbreeding territories and riffle length (Fig. 3) suggests that kingfishers may assess habitat quality (amount of food available) by observing the length of riffles present.

A "new" function of territoriality.—The view adopted in this study and held by most biologists is that territoriality evolved because defense of essential resources directly enhances the reproductive success of the defender (Nice 1941, Lack 1943, Hinde 1956, Brown 1964). But recently, it has been proposed that territorial behavior could also be adaptive by decreasing the success of one's reproductive competitors (Verner 1977). For example, if the cost of defense of a resource is minimal, the benefit in terms of relative reproductive success may be substantial if an individual can prevent conspecifics from obtaining a nest or food. A crucial assumption of the hypothesis of "superterritories" is that the cost of defense is not prohibitive. Along this line, Rothstein (1979) argues for the evolution of "inhibitory traits," like aggression, in animals that use specialized nest sites or utilize highly concentrated food resources. In the present study, 28% of the available nest sites appeared to remain unoccupied due to exclusion of potential nesters by extant territory owners. Such aggressive behavior, characteristic of territoriality in *Megaceryle alcyon,* could be an "inhibitory trait" as described by Rothstein. If so, territoriality in this species may be adaptive not only because it secures resources essential to survival, but also because it excludes competitors from resources that are not utilized by a defender.

Several investigators (Getty 1979, Pleasants and Pleasants 1979) have voiced strong criticism of this hypothesis. More empirical studies are needed to determine whether or not animals do defend territories larger than are needed to fulfill their own requirements. More extensive data on reproductive success and territory size are required, and animals that have specialized nest-site or food requirements that are easily defended should be critically evaluated.

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