COMPARATIVE FEEDING ECOLOGY OF TWENTY-TWO TROPICAL PISCIVORES

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ABSTRACT. Twenty-two fish-eating predators on a Peruvian lake show differences in hunting technique, habitat use, prey sizes, and prey species. The swimming predators take mostly different prey species. Waders differ in their prey species and sizes, and in the habitats in which they hunt. Perchers and cruisers hunt from different heights and take prey of different sizes and species. Many of the same types of differences are evident between groups using different hunting techniques, although several species pairs have remarkably similar diets.

RESUMEN. Veintidos depredadores de peces en un lago de Perú muestran diferencias en las técnicas de pesca, uso del habitat, tamaño y especies de las presas. Los depredadores nadadores, atrapan mayormente diferentes especies de presas. Las aves zancudas difieren en las especies y tamaños de las presas así como en los habitats en los cuales pescan. Aves que se posan para pescar ("perchers") y otras que recorren mucha distancia en su búsqueda por presas ("cruisers") pescan desde diferentes alturas y atrapan presas de diferentes tamaños y especies. Son evidentes muchas diferencias del mismo tipo entre grupos que usan distintas técnicas de pesca, aunque varios pares de especies tienen dietas remarcablemente similares.

Most comparative studies of potentially competing species have considered only closely related species on the assumption that morphological differences between those more distant insure relatively great differences in resource use. Root (1967) suggested that functional rather than taxonomic relationships are more important and that all species using the same class of resources should be considered because very different species can use the same resources.

In lowland Peru, oxbow lakes attract many fish-eating species that use a variety of hunting techniques. Some of these piscivores wade, some swim and pursue prey under water, some dive from flight, others dive from perches, and one skims the surface. Little information has been published on many of these species, and even those that are well known in some parts of their ranges are poorly known in South America. In this paper, I compare the feeding habits of twenty bird, one mammal, and one reptile species that I saw capture fish, and I analyze behavioral and ecological relationships within this portion of the fish-eating community.

STUDY SITE AND METHODS

Observations were made at Cocha Cashu, an oxbow lake of the Río Manu, in Manu National Park, Department of Madre de Dios, Peru, elevation about 350 m. The lake is 2 km long and about 100 m wide. During the periods that I was present, mostly in the late dry season, the lake reached a maximum depth of about 3 m. The water is murky, and the bottom is soft and silty.

I made observations in July and August, 1975, and August through December, 1976. I watched the members of the fish-eating community that regularly bring their prey to the water's surface. For size reference, weights for birds other than kingfishers (from Haverschmidt 1968) and the otter (from Duplaix 1980) are included in the following list. My own measurements for kingfishers are in Table 3. The species for which I gathered information are: Olivaceous Cormorant (*Phalacrocorax olivaceus*; 1113–1400 g), Anhinga (*Anhinga anhinga*; 1115–1250 g), White-necked Heron (*Ardea cocoi*; 1465–1750 g), Great Egret (*Casmerodius albus*; 770–1022 g), Green-backed Heron (*Butorides striatus*; 142–214 g), Snowy Egret (*Egretta thula*; 277–335 g), Chestnut-bellied Heron (*Agamia agami*; 565 g), Rufescent Tiger-Heron (*Tigrisoma lineatum*; 630–980 g), Capped Heron (*Pilherodius pileatus*; 444–632 g), Boat-billed Heron (*Cochlearius cochlearius*; 577–642 g), Black-collared Hawk (*Busarellus nigricollis*; 710–829 g), Osprey (*Pandion haliaetus*; 1440–1600 g), Large-billed Tern (*Phaetusa simplex*; 219–275 g), Yellow-billed Tern (*Sterna superciliaris*; 176–226 g), Black Skimmer (*Rynchops niger*; 222–377 g), Ringed Kingfisher (*Ceryle torquata*), Amazon Kingfisher (*Chloroceryle*

TABLE 1

MAXIMUM DAILY COUNT OF FISH-EATERS ON COCHA CASHU[1]

Phalacrocorax	17	*Pandion*	2
Anhinga	4	*Ceryle*	6
Ardea	3	*Chloroceryle amazona*	4
Casmerodius	4	*C. americana*	5
Egretta	1	*C. inda*	13
Butorides	11	*C. aenea*	3
Agamia	10	*Phaetusa*	5
Pilherodius	1	*Sterna*	6
Tigrisoma	14	*Rynchops*	4
Cochlearius	3	*Pteronura*	5
Busarellus	2		

[1] July–December.

amazona), Green-and-rufous Kingfisher (*Chloroceryle inda*), Green Kingfisher (*Chloroceryle americana*), American Pygmy Kingfisher (*Chloroceryle aenea*), Giant Otter (*Pteronura brasiliensis*; 24–34 kg), and Black Caiman (*Melanosuchus niger*).

I watched these species through 9× binoculars from a kayak and a dugout canoe, and through a 20× telescope from shore. I generally watched species as I encountered them and terminated observations when feeding stopped or when the subject moved from sight. When there was a choice between species, I chose the one for which I had the least information. The lakeshore was divided into discrete areas of open forest, brushy shrubs, grassy marshes, and dense stands of *Heliconia*. I recorded the habitat of all hunting birds, and if a bird moved from one habitat to another, I recorded its occurrence in both. Observations on any given day either covered the whole lake or half of it, with halves countered by the other half on another day so that habitats were censused approximately in proportion to their occurrences. I estimated prey lengths by comparison to known bill lengths. Perch and cruising heights were estimated by comparison to carefully gauged, strategically located landmarks. I sampled fish qualitatively using minnow traps, seine, throw nets, and hook and line; this allowed field identification of some of the prey species as they were captured by the birds. I censused fish-eating species by mapping daily sightings of individuals, and by counting birds as they arrived at lakeshore roosts in the evening. Mist-netting on the lakeshore, in the forest, and at an inland marsh provided additional information on population sizes and habitat use. Bill lengths and weights were taken for all netted kingfishers.

RESULTS

ABUNDANCES

The most common species were *Phalacrocorax, Chloroceryle inda, Tigrisoma, Butorides,* and *Agamia* (Table 1). No accurate census was possible for caimans, but they were extremely numerous. Numbers of several species, particularly *Phalacrocorax, Butorides,* and *Agamia* were augmented by arrival of immatures. Anhingas were absent from mid-August to early November. *Sterna* left the area by late October. Most *Phaetusa* left by late November; their disappearance coincided with feeding independence of their young and with rising water levels as the rainy season approached. *Egretta* and *Pilherodius,* both common in the backwaters of the Río Manu, only appeared on the lake when the river level was high. Two families of otters occasionally used the lake. They generally remained for only a day or two, often with several weeks between visits.

HUNTING BEHAVIOR

Five general classes of hunting behavior were used by the piscivores in this study: (1) swimming and diving from the surface; (2) wading; (3) diving from a perch; (4) cruising and diving from flight; (5) skimming. Within these classes there were some differences between species in details of hunting style, in prey sizes and species captured (Fig. 1) and in habitat use (Fig. 2).

(1) Swimming.—Anhingas and caimans hunted solitarily. Cormorants hunted either alone

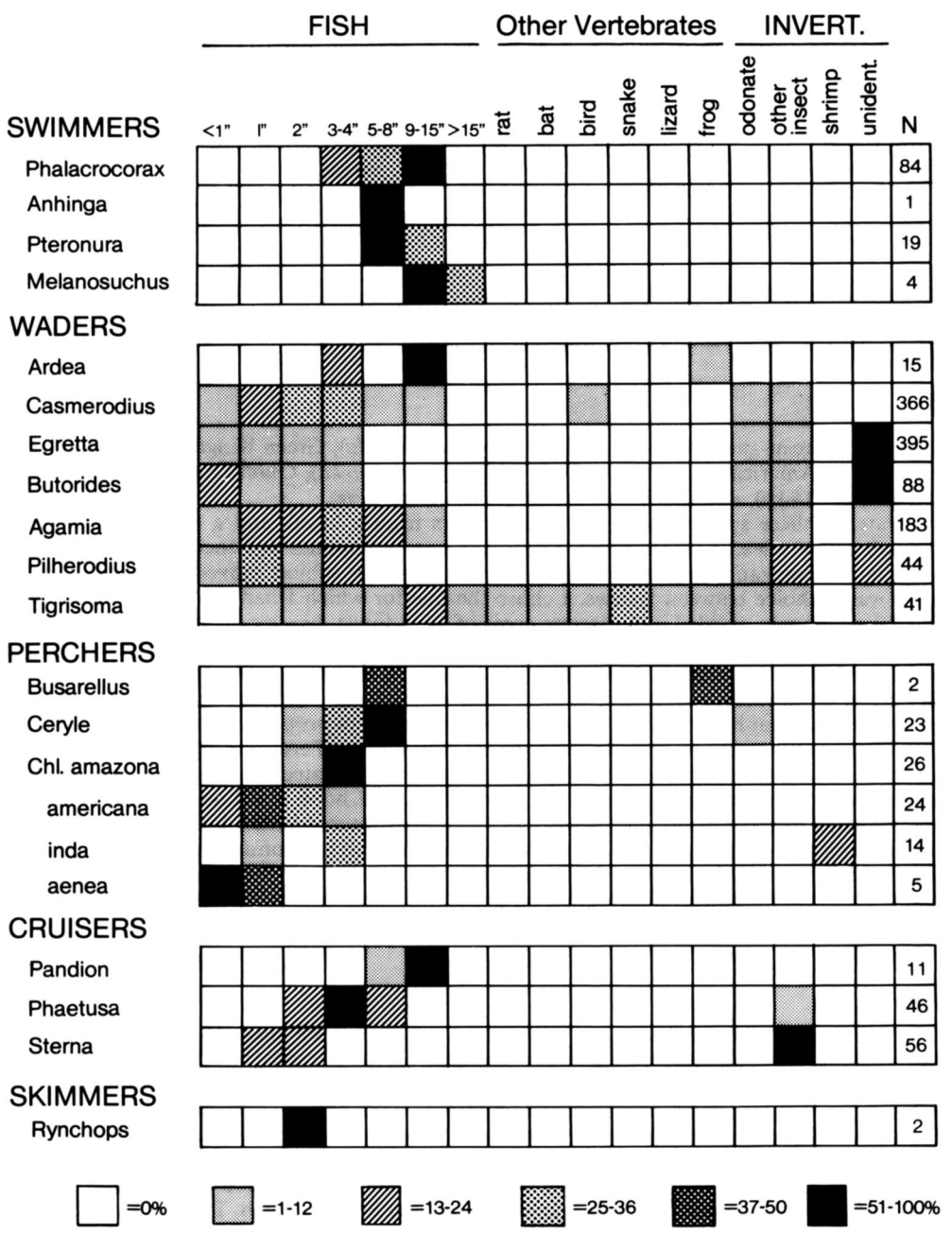

FIG. 1. Diets of Cocha Cashu fish-eaters.

or in small groups. Giant Otters were almost always in groups of 3 to 5. Anhingas, cormorants, and otters all pursued prey under water, whereas caimans waited quietly in shallow water, capturing fish by sudden ambush.

Cormorants took prey covering a broad range of sizes. Because I could not see prey that was swallowed under water or as a bird surfaced, my sample may be biased toward large and hard to handle fish. Sixty percent of the observed prey items were sedentary, shallow-water Loricariid catfish in the genera *Loricariichthys* and *Loricaria*. Most otter prey was large *Pla-*

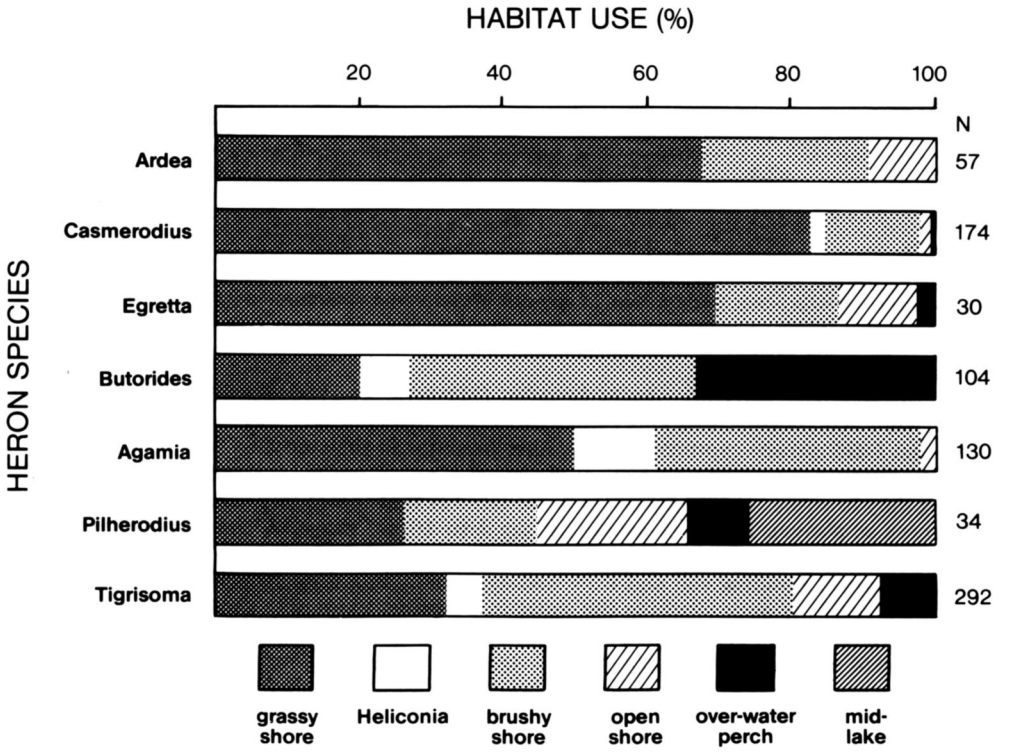

FIG. 2. Hunting habitats of Cocha Cashu herons.

gioscion squamosissimus (family Sciaenidae), a species I only captured in the deepest water of the lake. The four caiman prey recorded were Loricariid catfish in the genera *Hypostomus* and *Pterygoplicthys*. These were the largest fish prey observed in the study, and all were caught by caimans larger than 1 m. The total range of caiman prey must await observation of prey caught by the many small caimans also present.

(2) Wading.—Tigrisoma hunted by standing alert and motionless for long periods, moving only after a strike or a particularly long period of no activity. When prey was sighted, a bird pointed its bill toward it, and began slowly, almost imperceptibly bending toward it. Strikes were extremely powerful, often appearing to damage prey more severely than did strikes by other heron species. *Tigrisoma*'s diet was the most generalized of any species' in the study, with several snake species (individuals = 15–20 cm long) the most common prey. This heron was also one of the most generalized in habitat use.

Ardea largely restricted its hunting to the edges of grassy marshes. It hunted exclusively by slow wading mixed with long motionless periods, a hunting style almost identical to that of

TABLE 2

MEAN SEARCH TIME OF PERCHERS PER HUNTING PERCH[1]

	Mean	s.d.	N
Chloroceryle aenea	0.7	0.3	7
C. americana	1.5	1.9	48
C. inda	4.0	3.7	23
C. amazona	6.0	7.6	148
Ceryle torquata	12.0	12.9	101
Busarellus	59.0	15.0	4

[1] Time in minutes. All pairwise differences between means significant at $P < 0.025$ or less by Mann Whitney *U*-test.

TABLE 3

BILL LENGTH AND BODY WEIGHT OF KINGFISHERS[1]

	Bill			Weight		
	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N
torquata	62.4	3.7	7	303.6	20.1	8
amazona	53.7	2.1	6	114.5	6.7	6
inda	41.5	1.7	24	53.6	4.1	33
americana	34.0	2.0	5	29.0	.8	7
aenea	24.2	1.4	14	13.3	.9	22

[1] Bill length = nostril to tip, in mm. Weight in grams. All pairwise differences between means significant at $P < 0.001$ by Mann Whitney *U*-test.

its North American congener, *Ardea herodias* (Meyerriecks 1960; Kushlan 1976a; Willard 1977). More than half of *Ardea*'s prey was 20 to 35 cm long *Hoplias malabaricus* (Erythrinidae), a fish that I did not see captured by any other predator in the study.

Casmerodius also hunted primarily at the edges of grassy marshes. It waded slowly, usually pausing only to strike. This technique was the same as that commonly used in North America (references as above). Prey was mostly in the 2 to 10 cm range. A cichlid (*Aequidens* sp.) comprised 33 percent of the identified prey.

Agamia mixed standing still and slow wading, usually in a deep crouch with belly feathers and the curve of the neck touching the water in a manner extremely similar to the crouched waiting that Tricolored Herons frequently use (Willard 1977). From its crouch, *Agamia* made strikes toward prey near the water's surface. *Agamia*'s extremely long bill (150 mm) appeared to allow strikes at greater distance from its body than were possible for similarly sized herons with shorter bills (as suggested by Hancock and Elliot 1978). This may be especially important for striking around, over, and under the many protruding twigs in the tangled, flooded brush where *Agamia* often hunted. *Agamia* took prey primarily of 2 to 10 cm, and 52 percent of the identified prey items were Characidae, particularly *Triportheus angulatus* and *Astyanax* sp., both commonly observed surface species.

Butorides, Egretta, Pilherodius, and probably *Cochlearius* were small prey specialists with a mixed diet of 1 to 10 cm fish and invertebrates, many of which were too small to identify before being swallowed. *Butorides* hunted either by wading in shallow water under dense brush or by perching on protruding branches over open water. It moved along perches, sometimes perching at water level and pecking for prey there, sometimes climbing short distances above the water and either hanging acrobatically from the perch to grab at prey or plunging into the water. Similar behavior for other races of the Green-backed Heron has been described by Meyerriecks (1960) and Snow (1974). The feeding style of *Egretta* was varied and generally active, with a mixture of slow walking, running, foot-stirring and wing-flicking (follows Kushlan 1976a). Its hunting was largely restricted to grassy shores. *Pilherodius*' primary hunting style on Cocha Cashu was haphazard rapid pecking with no apparent orientation toward individual prey items ("sandpiper-style pecking": Willard 1977). An extreme incident of this behavior involved 789 probing strikes in 56 min, with only seven strikes apparently successful. Remsen (in press) also observed this feeding style in Colombia. *Pilherodius* also hunted by slow walking and sometimes employed aerial hunting. Birds sallied out and hovered over the water, striking for fish and swallowing in flight. Occasionally birds landed on the water and struck while swimming. They also hunted from perches at shoreline, and I saw one hunt by bill-vibrating (Kushlan 1973). *Cochlearius* was a nocturnal hunter. Its activity coincided with a nightly emergence of insects that attracted myriads of small fish (*Moenkhausia*) to the surface. Neither the fish nor the insects were evident during the day when other herons were hunting. At Cocha Cashu, feeding of *Cochlearius* appeared to be tactile (Willard 1979).

(3) Perching.—Hunting behavior of the five kingfishers and *Busarellus* involved sitting on a perch and plunging into the water for prey. The kingfishers took prey with their bills and swallowed it whole, while the hawk captured prey with its feet. Its hooked bill, used for tearing, allowed it to take prey too large to swallow whole. The hunting styles of these six species differed primarily in activity level. The mean length of time per hunting perch increased with size of the birds (Tables 2, 3).

Mean prey sizes of the perchers increased from the tiny prey of *C. aenea* to the relatively

TABLE 4
PERCH AND CRUISING HEIGHT[1]

	Perch height				Cruising height		
	$\bar{X}$	s.d.	N		$\bar{X}$	s.d.	N
Ceryle torquata	10.0	4.7	203	*Sterna*	3.0	4.9	51
Chloroceryle amazona	6.9	3.8	207	*Phaetusa*	10.3	4.3	26
C. inda	4.9	4.2	111	*Pandion*	13.0	6.5	13
C. americana	2.9	4.7	110				
C. aenea	1.4	.9	24				

[1] Values given in meters. All pairwise differences between means within groups significant at $P < 0.01$ by Mann Whitney *U*-test.

large fish and frog recorded for *Busarellus*. *Ceryle* and *C. amazona* took the most similarly-sized prey of the perchers. Thirty-five percent of *Ceryle*'s prey was the cichlid *Aequidens* sp., which *C. amazona* rarely took, whereas 65 percent of *C. amazona*'s prey was Characidae, particularly *Triportheus angulatus* and *Astyanax* which were rare in *Ceryle*'s diet.

Ceryle, Chloroceryle amazona, and *C. americana* used open perches and dived into open water. *Chloroceryle inda* and *C. aenea* occasionally hunted in the open, but more generally perched in shoreline brush and dived for prey underneath. They also used swampy forest and heavily wooded streams where the other species rarely ventured. *Busarellus*' favored haunts were coves choked with water weeds. The only kingfisher regularly found in these spots was the tiny *C. aenea*.

The kingfishers show a regular size gradient (Table 3). Bill lengths increase approximately 10 mm from one species to the next, and weights approximately double until the somewhat larger jump between *C. amazona* and *Ceryle*. Although perch heights overlapped somewhat, mean perch height increased with increasing kingfisher size (Table 4). At over 700 g, *Busarellus,* which perched in the height range (1–3 m; $\bar{X} = 1.3$ m; $N = 14$) of the three smallest kingfishers, does not fit this sequence.

(4) Cruising.—The two terns and Osprey hunted by cruising over the lake, and hovering and plunging after spotting prey. The three species cruised at different heights above the water (Table 4). Like kingfisher perch height, cruising height increased with size of the bird.

Most Osprey prey items were fish larger than 20 cm, primarily *Prochilodus* sp. (Prochilodontidae). *Phaetusa* took 5 to 15 cm fishes, mostly *Triportheus angulatus* and *Astyanax*. David Duffy (pers. comm.) and I each once observed *Phaetusa* skimming the surface in a manner similar to Black Skimmer feeding. Remsen (in press) also observed this once in Colombia. *Phaetusa* occasionally hunts at night, and determining the extent to which it uses skimming will require extensive night observations. *Sterna* took unidentified fishes, mostly 5 cm or smaller. It also swooped to the surface and dipped its bill for surface prey (probably insects) and made sudden upward sallies for flying insects. Mixed bill-dipping and aerial hunting accounted for 59 percent of my feeding observations of *Sterna* ($N = 131$).

(5) Skimming.—Black Skimmers, like *Cochlearius,* hunted nocturnally when the small fish *Moenkhausia* was active at the surface. The only two prey items I could identify with certainty were both this fish. All observed hunting was by skimming the surface with bill, snapping it shut on contact with prey.

TABLE 5
PREY CAPTURE RATES[1]

Ardea	.01 (11/864)	*Ceryle*	.003 (4/1304)
Casmerodius	.16 (332/2067)	*Chloroceryle amazona*	.02 (15/965)
Egretta	1.17 (317/270)	*C. inda*	.02 (2/92)
Butorides	.15 (60/405)	*C. americana*	.09 (6/67)
Agamia	.08 (152/1875)	*C. aenea*	.7 (2/3)
Tigrisoma	.008 (15/1788)		
Pilherodius	.19 (18/96)		

[1] Prey items/minute hunting time.

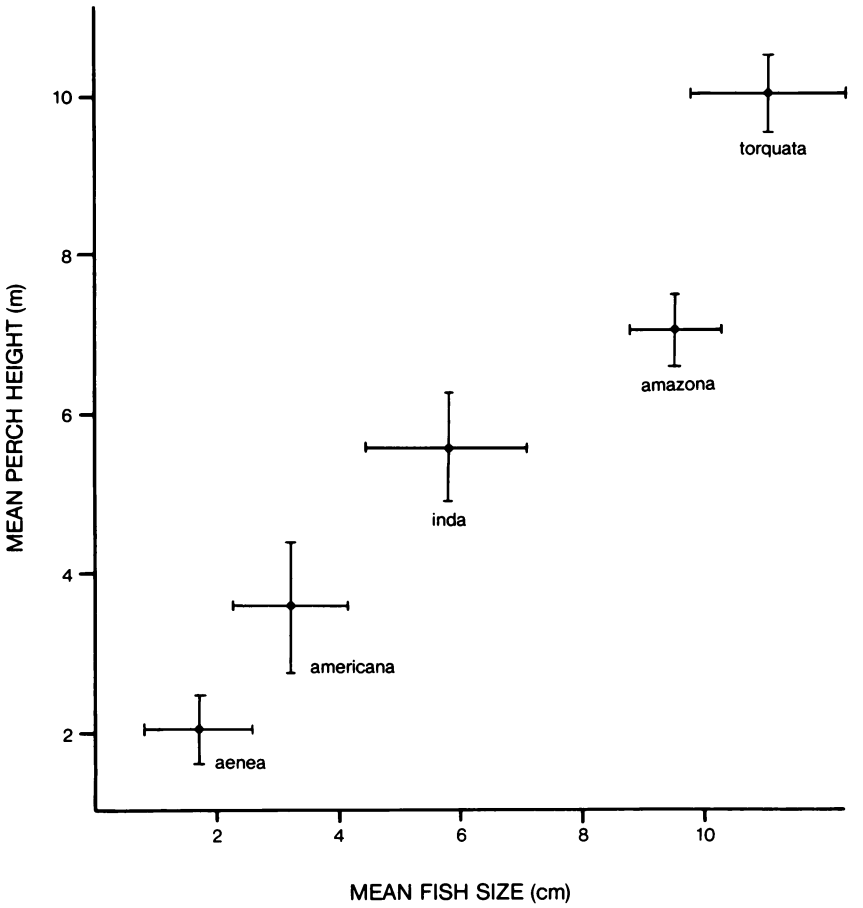

FIG. 3. Relationship between mean perch height and mean prey size of kingfishers. Vertical and horizontal lines indicate two standard errors on either side of the means.

PREY CAPTURE RATE

Among herons and kingfishers, species that took larger prey had lower capture rates. Between species in these groups that took equivalently-sized prey, the heavier herons always had the greater capture rates (Table 5).

DISCUSSION

PERCH AND CRUISING HEIGHT

MacArthur (1972) suggested that *Chloroceryle americana* perches near the water's surface in order to see the small fish that it is equipped to catch with its small bill. The larger *Ceryle,* because of its demands for greater absolute food intake, must perch higher to survey a greater area. On these high perches, it can no longer efficiently locate and capture small fish, but instead captures larger fish with its larger bill. MacArthur's argument is interesting in the context of the Cocha Cashu kingfisher community, where mean perch height and mean prey size are linearly related (Fig. 3).

The much larger *Busarellus,* while taking larger prey than any of the kingfishers, perched in the height range of the three smallest. It may be that the weedy coves where it habitually hunted cannot be effectively surveyed from higher perches. Although I saw only two prey items of *Busarellus,* I suspect that most of its prey is large because of the bird's large size and low capture rate (one prey item in 235 min of timed observation), and because it is not restricted to prey that it can swallow whole. This is supported by Remsen's (in press) observations of four captured fish ranging from 102 to 203 mm.

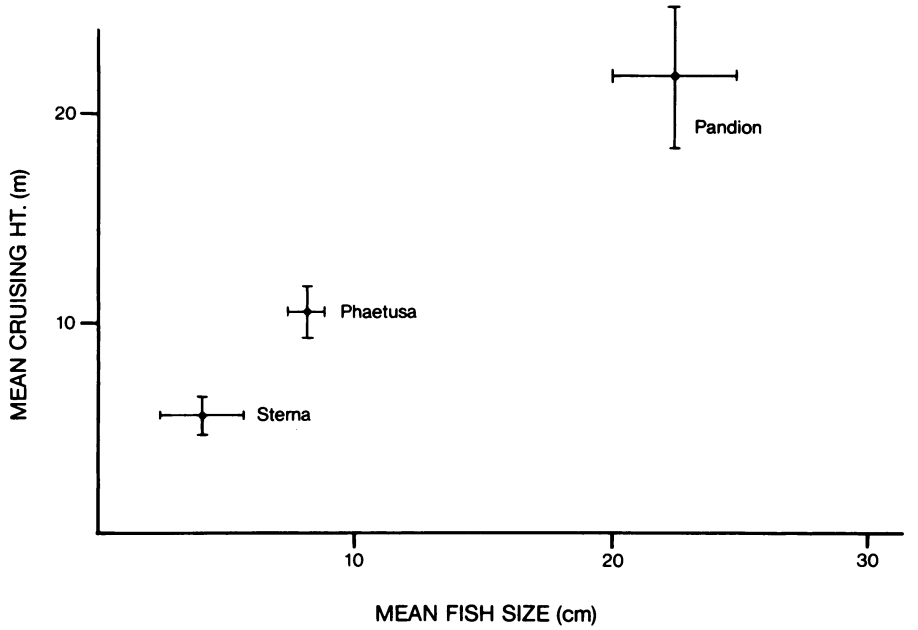

FIG. 4. Relationship between mean cruising height and mean prey size of terns and Osprey. Vertical and horizontal lines indicate two standard errors on either side of the means.

The relationship between cruising height and prey size in the two terns and Osprey (Fig. 4) shows a trend similar to that found for perch height and prey size in kingfishers.

SIMILARITY IN DIETS

Seven species (*Ardea, Tigrisoma, Pandion, Busarellus, Pteronura, Phalacrocorax,* and large *Melanosuchus*) took large prey, but showed virtually no overlap in their primary prey species. By contrast, the birds that took moderately-sized prey, had greater similarity of prey species. *Agamia, Chloroceryle amazona,* and *Phaetusa* all preyed heavily on the characins *Triportheus* and *Astyanax*; *Casmerodius* and *Ceryle* both took many of the cichlid *Aequidens.*

Populations of *Casmerodius* and *Agamia* may be near the carrying capacity of Cocha Cashu. Throughout this study, three *Casmerodius* hunted daily on the lake. I saw a fourth only once; each time it entered the water it was chased, even when the normal occupant was out roosting at the moment. *Agamia* populations also showed little fluctuation. The influx of young birds was short-lived, and, presumably, these were birds that had been fed by the adults normally present. If there were a superabundance of fish available for these herons, one would expect to see more fluctuation in their numbers.

Agamia captured prey four times as often as did *Chloroceryle amazona,* and *Casmerodius* captured prey 50 times as often as did *Ceryle.* If, in fact, Cocha Cashu heron populations are near carrying capacity, and if prey capture rates reflect food requirements of the birds, then even if diets, habitats, and hunting times were identical, the lake could support four *C. amazona* and 50 *Ceryle* with the food required by one additional *Agamia* or *Casmerodius.* The argument is obviously over-simplified, for there were some obvious dietary differences, particularly between *Casmerodius* and *Ceryle.* Nevertheless, the argument suggests the possibility of coexistence between two species with very similar diets, when one species consumes many fewer prey items, thus allowing several individuals of the less demanding species to survive where a single individual of the more demanding could not.

Phaetusa, while capturing many of the same prey species as *Agamia* and *Chloroceryle amazona,* often took them at mid-lake where they were not available to the other two. *Phaetusa*'s hunting style involved searching the whole lake for fish that happened to be at the surface at a given moment, whereas *Agamia* and *C. amazona* hunted smaller areas, waiting for prey to come within striking range.

The species that specialized on small prey had mixed diets of fish and invertebrates that I

usually could not identify. *Sterna* hunted mostly at mid-lake where its prey was inaccessible to the others. The small kingfishers rarely hunted along the dense grassy shoreline that constituted *Egretta*'s main hunting area, probably because of lack of satisfactory perches there. *Pilherodius*' shoreline feeding resulted in smaller prey than much taken by *Chloroceryle inda* and *C. americana*; its mid-lake prey were not accessible to these low perching kingfishers. *Butorides,* which hunted in the open and amid dense brush, was similar to *C. inda* and *C. americana* both in its habitat and vertebrate prey sizes. It captured many more invertebrate prey than I saw for either kingfisher. *Chloroceryle aenea*'s small size allowed it to enter vegetation that was not open to any other Cocha Cashu fish-eater. Its total range of prey sizes was the smallest of any of the species.

Other Fish-eating Communities

Remsen (in press) concentrated primarily on kingfishers, but also observed other fish-eating birds. The regular fish-eaters in his Colombian and my Peruvian communities were the same, and, although our observations differed somewhat, particularly in kingfisher perch heights and prey sizes, our conclusions regarding resource use are very similar. We observed the same trends in prey size differences and many of the same habitat and behavioral differences.

Whitfield and Blaber (1978, 1979a, b) studied 10 members (three swimmers, four waders, and three cruisers) of a fish-eating community on a large East African lake. They did not mention what other fish-eaters were present, so a species by species comparison between their site and Cocha Cashu is not possible. Dietary differences based purely on prey sizes appeared to be more prevalent in the African community, although this might not be so if additional members were considered. Several common prey species appeared to be more generally used than was any single prey species at Cocha Cashu, where differences in prey types were more prevalent.

Whitfield and Blaber (1979a) suggested that tarsometatarsal length determined the fishing depths of the waders and, thus, indirectly, the sizes of fishes available to them. Other studies of wading bird communities (e.g., Kushlan 1976b; Willard 1977) have also suggested a fishing depth component of resource segregation. At Cocha Cashu, all herons restricted their hunting to very shallow water and had relatively minor hunting depth differences. In fact, the smallest heron, *Butorides,* hunted in the deepest water when it used protruding perches. One possible explanation for the differences between these studies is that the common presence of caimans at Cocha Cashu restricts herons to shallow water from which they can escape easily and in which large caimans cannot maneuver well. In deep water, with attention strongly focused on potential prey, even the largest herons may run the risk of becoming prey themselves.

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