

COMMENSALISM IN THE LITTLE BLUE HERON

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ABSTRACT.—Little Blue Herons feed in association with White Ibis by using the ibis's movements to increase foraging effectiveness. When feeding near a White Ibis, a heron increased the number of prey caught without increasing its energetic costs of foraging. The strike rate of a bird was higher when feeding commensally than when feeding alone, but its success per strike did not increase because of the commensal association. This increased energy return when feeding commensally resulted from greater opportunity for commensal herons to observe and attempt to catch prey rather than from an increased probability of their catching a prey item after it had been observed. The results of this study of a non-obvious commensal relationship suggest that many previously reported associations among water birds are also commensal. It also supports the hypothesis that multispecies aggregations of ciconiiforms may be characterized by cryptic forms of commensalism. Received 30 August 1977, accepted 15 January 1978.

SYMBIOTIC relationships are widespread among animals. In birds, multispecies foraging associations range from those that are casual and short-lived to those that are highly evolved and persistent (Rand 1954). I have previously shown that ciconiiform wading birds form foraging aggregations through the social signalling of white plumaged core species (Kushlan 1977a) and that such aggregative feeding may be of considerable ecological importance (Kushlan 1976a). I have further suggested that ciconiiform aggregations may involve cryptic forms of commensalism or mutualism (Kushlan 1978). In this paper I explore this possibility by analyzing a two-species association between Little Blue Herons (*Florida caerulea*) and White Ibis (*Eudocimus albus*). I also consider the mechanisms by which commensal advantages can be obtained and the probable extent of the existence of loose commensal associations among aquatic birds.

The White Ibis provides an excellent model of a passive core species in that it forms monospecific flocks, is highly conspicuous, participates in mixed-species aggregations, and is relatively passive in foraging (Kushlan 1977b). Courser and Dinsmore (1975) noted the possible use of White Ibis by Snowy Egrets (*Egretta thula*) and Louisiana Herons (*Hydranassa tricolor*) but their data failed to demonstrate that the associations were commensal. The Little Blue Heron is a good model of an attendant species in an association in that it forages in dispersed monospecific aggregations often peripheral to major bird concentrations. Its slow-walking foraging technique might permit it to take advantage of prey made available by other birds foraging nearby. The relation between White Ibises and Little Blue Herons within their aggregation is not immediately obvious and so is a good test to distinguish between commensal and non-commensal potentials of a relatively simple mixed-species feeding aggregation.

METHODS

The study was conducted in the Everglades of southern Florida during March 1976. The birds were feeding in sparse marsh vegetation of sawgrass (*Cladium jamaicensis*), spikerush (*Eleocharis cellulosa*), and pickerelweed (*Pontedaria lanceolata*). The assemblages moved over an area of about 1 ha during the period of observation. Visibility was good owing to the open nature of the habitat.

To eliminate the potentially confounding effects of the variability of habitat, weather, and food from one place or one time to another, data were collected pairwise at a single location. Sequential 1-min

observations were taken on one heron foraging near a White Ibis and then immediately on another heron feeding independently within 100 m and in the same habitat as the first. The number of fishing strikes, successful attempts, and steps taken were tabulated for each heron during the sample period. Potentially commensal herons were distinguished by being less than 1 m from an ibis at the beginning of the observation period. Independently feeding birds were more than 10 m from an ibis at the beginning of the observation period and never moved to within 1 m of an ibis while being observed. Forty-six paired data sets were tested by Wilcoxon signed rank test at $P < .05$ using the normal approximation (Siegel 1956). Feeding behaviors discussed are described by Kushlan (1976b, 1977b).

RESULTS

The size of the feeding assemblage varied with the arrival and departure of individuals. It contained on the average 75 adult White Ibis and 30 adult Little Blue Herons. No immature Little Blue Herons participated in the aggregation. White Ibis fed by deep probing around plant clumps and by step-probing, a technique in which the bird moves immediately after a shallow probe. Little Blue Herons fed visually by walking slowly in upright or crouched position. At any time about 75% of the Little Blue Herons were foraging near a White Ibis. The approach of a heron to an ibis often appeared deliberate. Upon arriving at the ibis, the heron walked behind or at the ibis's side and followed it for a short time. There was no dramatic change in the heron's slow walking foraging behavior when it began to feed near an ibis. The heron would deviate from the ibis's path to pursue its own course, often after apparently spotting something or someplace that merited its further attention. A heron directed its attention to such a place by examining it closely, often by head-tilting and neck-swaying.

Little Blue Herons feeding with White Ibis and those feeding alone both caught small fish 1–2 cm in length. As they swallowed such small prey almost instantaneously there was little opportunity to observe prey size. However, no fish caught was longer than 2 cm and it is reasonable to assume that there were no major differences in the size or quality of prey taken by Little Blue Herons feeding near and those feeding away from ibis and that the energy return per catch was relatively constant. If this is so, the foraging return to herons can be indexed by the number of fish caught per minute of foraging. Little Blue Herons feeding near White Ibis caught twice as many fish per foraging period as those feeding alone (Table 1). The differences between paired comparisons were significantly different ($P < .05$). Thus feeding near an ibis appeared to confer an advantage to a heron in terms of its gross energy intake.

Heron did not achieve this higher intake near White Ibis by being more successful per attempted capture, as the success rate (catches per stab) was the same for both categories of herons. However, herons feeding near ibises made more stabs (attempted captures) per minute than did herons feeding independently (Table 1). Thus, the herons obtained more prey per minute feeding near ibises because they attempted more captures, probably because ibis made prey more visible.

The effort expended by foraging Little Blue Herons can be estimated by the number of steps a bird took per minute. By this measure, the energy expended by a heron was the same whether it fed with or away from an ibis (Table 1).

DISCUSSION

Nature of the association.—The Little Blue Heron–White Ibis association is commensal, with the heron benefiting by foraging near an ibis. The heron obtains more

TABLE 1. Mean and range of foraging parameters and rank statistics of paired observations of Little Blue Herons foraging near and away from White Ibis. W is the Wilcoxon statistic. Z is the standard normal random variable using a normal approximation

	Mean (range)		Statistics			
	Near ibis	Away from ibis	N	W	Z	P
Catches/min	0.8 (0-4)	0.4 (0-3)	27	206.5	2.49	<.05
Catches/stab	0.8 (0-1)	0.8 (0-1)	23	49.0	1.45	NS
Stabs/min	1.4 (0-4)	0.9 (0-4)	31	230.0	2.32	<.05
Steps/min	29.5 (11-44)	28.3 (11-46)	45	82.5	0.46	NS

energy per foraging time with no apparent increase in its energy expenditure. My observations suggest that the ibis receives no benefits from the heron's presence. When a heron came close to an ibis's head, the ibis often attacked with an open-billed lunge. The heron-ibis commensal association is weak compared with, for example, the association of Cattle Egrets (*Bubulcus ibis*) with cattle, a highly evolved relationship that includes foraging benefit to Cattle Egrets (Heatwole 1965), interspecific cleaning (Dawn 1959, Snoddy 1969), communication by warning flights (Rice 1954), and movement provocation (Dawn 1959). Whereas a Cattle Egret remains in close attendance upon its commensal, a Little Blue Heron moves in and out of close proximity to an ibis responding to potential feeding opportunities.

Opportunities abound for wading birds and other water birds to participate in commensal associations. Diverse associations among coots, ducks, gallinules, grebes, avocets, and phalaropes have been reported (e.g. Williams 1953, Ashmole, et al. 1956, King 1963, Paulson 1969, Siegfried 1971a, Siegfried and Batt 1972, Anderson 1974), but increased foraging return to attending species has not yet been demonstrated quantitatively for most such associations. Among ciconiiforms, Snowy Egrets, Louisiana Herons, and Great Egrets (*Casmerodius albus*) attend mergansers (Christman 1957, Parks and Bressler 1963, Emlen and Ambrose 1970); Great Egrets, Snowy Egrets, and Little Egrets (*Egretta garzetta*) attend cormorants (Christman 1957, Fraser 1974); Little Egrets attend spoonbills (*Platalea alba*) (Reynolds 1965); Snowy Egrets and Great Egrets attend cattle (Rice 1954, Caldwell 1956); kingfishers forage near Snowy Egrets, Louisiana Herons, and Great Egrets (Parks and Bressler 1963, Meyerriecks and Nellis 1967); and grebes associate with Snowy Egrets and Louisiana Herons (Mueller et al. 1972). Leck (1971) reported cooperative feeding between Snowy Egrets and grebes, but his data did not demonstrate either cooperative or commensal feeding. Emlen and Ambrose (1970) stated without quantitative support that striking and capture rate increased when herons fed near mergansers. Thus, there are many observations but few data supporting the hypothesis that such reported water bird associations are commensal. That the somewhat cryptic association discussed in this paper provides an energetic advantage to one of the participants suggests that many of the water bird associations noted by others probably are commensal also. The commensal nature of the two-species aggregation I studied also lends support to the concept that many wading bird aggregations involve commensal or mutualistic interactions (Kushlan 1978).

Tactics of commensalism.—There are two ways a commensally-feeding wading bird may increase the number of prey items taken per minute: (1) it could increase the proportion of successful stabs, i.e. its success rate; or (2) with the same success rate it could increase the total number of stabs taken. Most previous studies have not distinguished between these tactical possibilities. One might expect a priori that

the success rate (number of successful captures per stab) would increase in commensal feeding, and following this line of reasoning Rand (1954), Meyerriecks (1960), and Heatwole (1965) have suggested that commensal feeding and use of "beaters" make prey easier to catch. However, it is just as likely that commensal feeding, rather than making prey more vulnerable, increases the commensal's chance of locating a prey item. This would not change the probability of a potential prey being caught once observed, but would increase the number of attempted captures. Higher rates of feeding (attempted captures) are commonly reported in purported and proven cases of commensal feeding (Rand 1953, Paulson 1969, Emlen and Ambrose 1970, Smith 1971, Siegfried 1971b, Siegfried and Batt 1972, Dinsmore 1973, Anderson 1974). Increased feeding rates, but not necessarily greater success rates, may be a general characteristic of many commensal associations.

Whereas Little Blue Herons expend similar amounts of energy whether near or away from White Ibis, Cattle Egrets take fewer steps and so expend less energy near than away from cattle (Heatwole 1965, Dinsmore 1973, Grubb 1976). Both Cattle Egrets and Little Blue Herons forage by walking slowly until a potential prey item is observed, and then often pause to head-tilt or neck-sway in preparation for striking. It would seem that the more potential prey seen, the more attempts made, and the more pause time taken by commensal birds would result in fewer steps being taken per minute. This is apparently the case in Cattle Egrets but not in Little Blue Herons. Perhaps prey vulnerability differs for the two species such that Cattle Egrets are required to spend more pause time before strikes. The speed of movement of the beaters relative to the bird's own speed of movement may affect the energy requirements of a commensal bird. Cattle Egrets feeding with relatively slow moving cattle may take fewer steps than those feeding alone on pastureland. Little Blue Herons feeding in a shallow marsh follow an animal similar to their own size and both may walk at about the same speed. In this case the heron's speed would be similar with or without an ibis. The magnitude of the energy advantage associated with a commensal association may therefore depend on such factors as habitat, prey type and vulnerability, and speed of movement of the commensal.

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