

# Social Foraging by Waterbirds in Shallow Coastal Lagoons in Ghana

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**Abstract.**—Social foraging in waterbirds in Ghanaian coastal lagoons was studied during October and November 1994. Two types of foraging were social: directionally synchronized flocks (often involving distinctive feeding methods used in unison) and dense pecking aggregations. Social flocks were typically larger and denser than non-social flocks, and primarily involved piscivorous birds, especially the longer-legged shorebirds and egrets. It is probable that the flocks concentrate fish into temporarily high densities through herding or confusing escape reactions. We suggest that these flocks, rather than simply forming in areas of existing high prey density, may actively enhance their foraging success. There may be a true social element to either the initiation or persistence of waterbird social foraging flocks in coastal Ghana. *Received 14 June 2002, accepted 25 August 2002.*

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High-density feeding aggregations are well documented for herons and egrets, and are usually explained as forming in areas of high prey availability (Kushlan 1981). Proposed benefits include decreasing search time between patches of food items, increasing the likelihood of successful foraging in a suitable location, decreasing the risk of obtaining no food, and perhaps having more food available (Kushlan 1981). A general assumption is that individual birds locate a site with good feeding conditions, and flocks form at these sites. Egrets, for example, are attracted to other feeding birds (Smith 1995), or even models of birds (Kushlan, 1977; Caldwell 1981), perhaps because they signal high food levels. Capture rates or intake rates for birds have been shown to increase with flock size (Krebs 1974; Smith 1995), indicating either that social foraging affects foraging success or that better sites attract more birds. Flocking can vary in time as well as in space: Kersten *et al.* (1991) showed that Little Egrets (*Egretta garzetta*) in the Ca-

margue, France, formed feeding aggregations in the early morning. Overnight respiration by aquatic plants reduced the dissolved oxygen content of the water in small pools, and fish tended to move to the water surface (where the oxygen content was higher), where they were available to feeding egrets.

Some feeding flocks appear to have a social element. For example, Grimes (1969) described Spotted Redshank (*Tringa erythropus*) in Ghana feeding "in mass" with herons and egrets, Redshank (*T. totanus*), Greenshank (*T. nebularia*), and Marsh Sandpiper (*T. stagnatilis*). Spotted Redshank swam in close-packed rafts with apparently coordinated movements that, he presumed, helped to bring food to the surface. Boettcher *et al.* (1994) described the American Avocet (*Recurvirostra americana*) feeding with synchronized movements, apparently to flush or herd nektonic invertebrates. Aside from shorebirds, several other waterbirds feed in a

highly coordinated fashion, e.g. Little Black Cormorant (*Phalacrocorax sulcirostris*; Marchant and Higgins 1990), Great Cormorant (*P. carbo*; van Eerden and Voslamber 1995), Smew (*Mergus albellus*; Platteeuw *et al.* 1997), Red-breasted Merganser (*M. serrator*; Cramp and Simmons 1977), Goosander (*M. merganser*; Cramp and Simmons 1977), Spoonbill (*Platalea leucorodia*; Voslamber and Buijse 1996), and White Pelican (*Pelecanus onocrotalus*; Saino *et al.* 1995). Such aggregations are often called social feeding flocks, and it is possible that the birds themselves actively increase local prey availability through their foraging behavior. Experiments have shown that in the Black-headed Gull (*Larus ridibundus*), feeding success increased with flock size, partly because flocks split fish schools into smaller, more vulnerable, groups (Götmark *et al.* 1986).

In this study, the occurrence of social foraging on lagoons in coastal Ghana is quantified. Prey density could not be estimated well enough to determine whether social foraging flocks experienced higher prey availability than non-social flocks. However, behavioral evidence is presented to suggest that social flocks may have mechanisms to prolong their existence, suggesting that the birds do accrue real benefits.

#### METHODS

Flocking associations and behavior of coastal waterbirds were studied in October and November 1994 at Songor and Keta Lagoons (05°49'N:00°28'E and 05°55'N:00°59'E respectively), southeastern Ghana (see Ntiamao-Baidu *et al.* (1998) for full details and maps). Both lagoons are fed directly by rain, by freshwater from streams and rivers and through saltwater and freshwater seepage through the beach dunes. When water levels are low (as they were during this study) salinity can be very high (40-100 ppt).

The Songor wetland comprises a brackish-water lagoon with extensive mudflats and islands. A broad sandy beach separates it from the sea in the south and this is where our observations were concentrated, near the villages of Vunya and Totokpoe. The lagoon is bordered on the east and west by degraded and stunted mangroves, as well as coastal savannah vegetation. In the study period, maximum water depth was about 40 cm and most areas were less than 10 cm deep. The sediment of this lagoon is very fine and soft (see Piersma and Ntiamao-Baidu 1995 for details). The combination of shallow water, soft sediment, strong breezes and hu-

man foot-traffic through the lagoon resulted in very turbid water.

Keta is a large lagoon (up to 300 km<sup>2</sup>) near the border between Ghana and Togo. The water area was estimated at around 75 km<sup>2</sup> during our visit, with water depths of mostly less than 30 cm (although depths of 1.5 m occurred in the middle of the lagoon away from our study areas). Fieldwork was performed at three main sites: Fiahor, which had large dry mudbanks extending up to 1,500 m into the lagoon; Anloga, the site of a freshwater inflow and extensive *Typha*-marshes giving way to exposed mudflats at the lagoon proper; Tegbi, being the eastern end of mudflats extending from Anloga in the west. Water was 200-500 m from the lagoon margin, and afternoon breezes temporarily pushed water closer to the lagoon edge.

Observations were made using zoom telescopes (magnification 15-60×) during daylight, dusk and dawn, and with a Delnocta 5× night-scope during the hours of darkness. A small infrared light beam was used to enhance the clarity of the light-intensified image on the night-scope. The resolution gained with the night-scope was often too poor to yield reliable species identification and foraging observations, so data are fewer at night. When birds were distant at night, binoculars and telescopes were sometimes used under moonlight in preference to the night-scope. Regular scans were made during the day at the observation sites of all waterbird flocks, where a flock was defined as being individuals of any species within 20 body-lengths of another. Single birds were also treated as a "flock".

For each individual or sample of individuals, records were made of: (a) the species involved, (b) mix (number of species in the flock), (c) activity of individuals (categorized as feeding, comfort [preening, bathing] or roosting), (d) total number of individuals of each species in the flock, (e) mean number of body-lengths to nearest conspecific, (f) mean body-length to nearest neighbor regardless of species, and (g) mean water depth (estimated from exposed leg length, converted to depth from scale drawings or photographs). These data were used to characterize the habitat use and social behavior of the waterbird community at these sites (Piersma and Ntiamao-Baidu 1995; Ntiamao-Baidu *et al.* 1998). Sometimes at night and when flocks were distant, not all details could be noted, so sample sizes differ in the analyses depending on the variable. Morning and afternoon observation periods were alternated to ensure results over the daylight periods were unbiased.

Flocks were defined as "social flocks" when the foraging birds showed very directionally synchronized movements (see Grimes 1969; Zwartz 1974). Preliminary fieldwork revealed such flocks, often involving scything (sweeping of the bill from side to side) or plowing (running with the bill partially immersed at a low angle in the water). Large, very dense and noisy flocks were also frequently noted, in which birds typically pecked (quick jabbing of the bill into the water), and walked rapidly with no regard for the movements of other individuals. These flocks were also classified as social.

Distinctive feeding behavior in social flocks was recorded. Bird flocks were frequently large and spread-out and both social and non-social activities could occur within a given flock. For flocks with mixed feeding styles, social components are treated as constituting their own flock. These social flocks are compared with non-social feeding flocks. Total flock size refers to the

number of feeding birds (non-feeding birds are excluded from the analysis).

In the analyses, feeding guilds of waterbirds are defined on the basis of information on the feeding style and sensory mechanism (Piersma and Ntiamoa-Baidu 1995; Ntiamoa-Baidu *et al.* 1998). These are: (1) herbivorous ducks, (2) visual surface-foraging shorebirds, (3) tactile surface-foraging shorebirds, (4) pelagic-foraging shorebirds, (5) stalking herons, (6) fishing pelicans, and (7) fishing terns. Guilds 2-6 are involved in this study.

The fish fauna of the lagoons consists mainly of cichlids of several genera, collectively referred to as tilapia. These provide a food source for local villagers, and also for piscivorous birds, including egrets and certain shorebirds. The three fish-netting methods employed (Piersma and Ntiamoa-Baidu 1995) caught fish 0.5-8.0 cm in length (*Sarotherodon melanotheron* at Songor; *S. melanotheron*, *Oreochromis niloticus*, *Tilapia zillii*, *Hemichromis bimaculatus*, *H. faciatus* and mullet *Mugil* spp. at Keta). Occasionally egrets were observed taking larger individuals (up to c. 15 cm).

## RESULTS

### Feeding techniques

Pecking (a visual foraging technique) was the commonest feeding method used by social feeding flocks, and was the only method used by herons and egrets. Two other distinctive tactile social feeding methods were observed were plowing and scything. These methods were frequently used by the *Tringa* shorebirds (Greenshank, Marsh Sandpiper, Spotted Redshank and Redshank). In the few instances it was possible to follow a plowing bird visually for a couple of seconds or more (birds quickly became obscured, and these feeding runs are typically very fast), frequent captures indicated that this is a highly successful method when feeding on fish. When plowing, birds would usually run in a loose line consisting of a couple to c.15 individuals, and could cover 5-20 m in a run (long runs being noted in duos). Solitary birds and duos also plowed by night. Groups of plowing birds regularly broke away from the edges of dense pecking aggregations, strengthening our contention that these aggregations be treated as social flocks.

Scything was used less frequently than plowing in social flocks. It was especially prominent in the Avocet (*Recurvirostra avocetta*) and Spotted Redshank, but was seldom seen in non-socially feeding birds, except the

occasional Black-winged Stilt (*Himantopus himantopus*), a species for which scything is an uncommon feeding method in most areas (Pierce 1985).

### Occurrence of social foraging and species involved

We recorded 127 social foraging flocks, containing 8,300 individuals, and 2,346 non-social foraging flocks, containing nearly 56,000 individuals. Six shorebird species showed social foraging regularly (Table 1), most being pelagic foraging birds (Greenshank, Marsh Sandpiper, Spotted Redshank, Redshank, Avocet and Black-winged Stilt). Of the stalking herons (guild 5), both Little Egret and Reef Heron (*Egretta sacra*) often fed socially (Table 1). As elsewhere in Africa (e.g., Saino *et al.* 1995), social foraging was prominent in the White Pelican on Keta Lagoon, although we recorded it only on a few occasions at dusk (and only once during formal observations).

Social foraging was most often seen in Greenshank, Marsh Sandpiper, Spotted Redshank and Avocet (Table 1), with between 12% and 30% of all feeding flocks showing social elements. Greenshank and Marsh Sandpiper accounted for the majority of the social birds (19% and 51% respectively). In addition to Redshanks and Black-winged Stilts, three other shorebirds occasionally associated with social shorebird flocks: Wood Sandpiper (*T. glareola*), Bar-tailed Godwit (*Limosa lapponica*) and Curlew Sandpiper (*Calidris ferruginea*). Wood Sandpipers were regularly seen eating small tilapia; godwits and Curlew Sandpipers were worm-feeders and probably only coincidentally in the flocks. However, other probing waders such as Sanderling (*C. alba*) were seen actively feeding on small tilapia (albeit non-socially) at Songor. Egrets and herons also joined socially foraging shorebird flocks, though they sometimes instigated their own social flocks.

Most feeding flocks were composed of a single species, for both social and non-social flocks (Fig. 1). The mean flock mix did not differ between social and non-social flocks ( $1.7 \pm \text{SD } 1.3$  species for both flock types; t-test on log-transformed data,  $t_{2451} = 0.249$ ,

Table 1. Incidence of social foraging flocks at Songor and Keta Lagoons, October-November 1994. Species are arranged in decreasing order of the proportion of individuals that fed socially. The two "observed" columns refer to all flocks containing foraging birds. "Shank" spp. refers to any of Greenshank, Marsh Sandpiper, Spotted Redshank or Redshank; these flocks refer mainly to birds feeding at night when species could not be determined. Guilds were determined by Ntiamoa-Baidu *et al.* (1998).

Species	Number of		Number of individuals observed	Number of		Percent of flocks social	Percent of		Guild	Diet
	flocks observed	individuals observed		flocks social	individuals social		individuals social	individuals social		
White Pelican	3	246	1	240	33	98	6	fish		
<i>Fringa</i> spp.	28	967	16	587	57	61	4	fish		
Marsh Sandpiper	350	8,218	69	4,227	20	51	4	fish		
Avocet	43	2,206	7	830	16	38	4	fish		
Spotted Redshank	47	417	14	147	30	35	4	fish		
Greenshank	363	4,874	44	1,603	12	33	4	fish		
Little Egret	218	1,214	17	305	7.8	25	5	fish		
Redshank	157	644	11	61	7.0	9.5	2	fish, invertebrates		
Reef Heron	176	618	10	40	5.7	6.5	5	fish		
Grey Heron	67	323	1	19	1.5	5.9	5	fish		
Black-winged Stilt	426	3,929	9	225	2.1	5.7	4	fish, invertebrates		
Great White Egret	18	41	1	1	5.6	2.4	5	fish		
Bar-tailed Godwit	93	373	1	2	1.1	0.5	3	worms		
Wood Sandpiper	172	538	1	1	0.6	0.2	2	invertebrates		
Curlew Sandpiper	608	26,364	1	9	0.2	0.03	3	invertebrates, seeds		

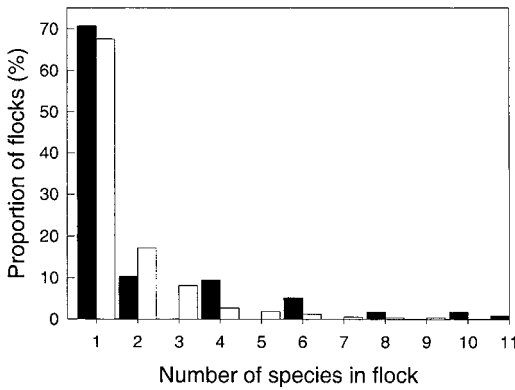


Figure 1. Number of species of waterbird in social and non-social feeding flocks in Songor and Keta Lagoons in October and November 1994. Dark bars are social flocks; pale bars are non-social flocks. N = 116 social flocks and 2,335 non-social flocks.

n.s.). The most diverse social flock contained seven species, and the most diverse non-social flock held eleven species (single flocks of 10 and 11 species are not shown in Fig. 1 for non-social birds).

Social feeding flocks were larger on average than non-social flocks (social flocks, mean =  $65.4 \pm$  (S.D.) 102.5 individuals, N = 127; non-social flocks, mean =  $23.8 \pm$  79.7 individuals, N = 2,348; t-test on log-transformed data,  $t_{2473} = 11.6$ ,  $P < 0.001$ ) (Fig. 2). Greenshank and Marsh Sandpiper provided the bulk of individuals in the larger flocks.

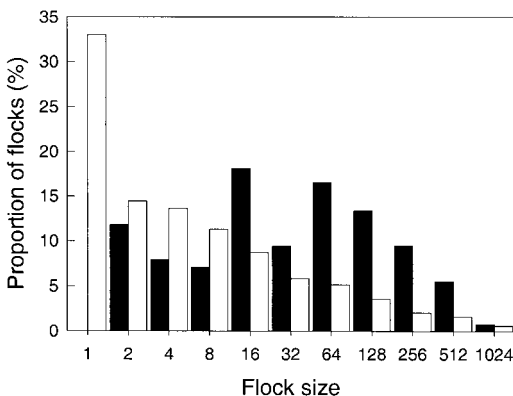


Figure 2. Sizes of social and non-social feeding flocks in Songor and Keta Lagoons in October and November 1994. Dark bars are social flocks; pale bars are non-social flocks. N = 127 social flocks and 2,346 non-social flocks. Note that bars double in magnitude along the x-axis.

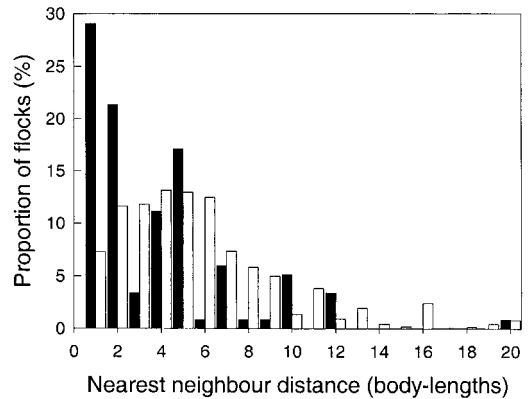


Figure 3. Mean nearest neighbor distance of foraging birds in social and non-social flocks in Songor and Keta Lagoons in October and November 1994. Nearest neighbor distance is in body-lengths, weighted by the number of individuals in each species in the flock. Dark bars are social flocks; pale bars are non-social flocks. N = 122 social flocks and 1,644 non-social flocks.

Social flocks were strikingly dense (Fig. 3). Over half the social flocks had a nearest neighbor distance of one body-length or less (weighted averages of the individual species in the flock), and the least dense was only 8.4 body-lengths (mean =  $1.6 \pm 1.3$ , N = 123). Non-social flocks were much less dense (mean =  $4.9 \pm 3.7$ , N = 1,646; t-test on log-transformed data,  $t_{1767} = 14.0$ ,  $P < 0.001$ ).

For both social and non-social flocks, larger flocks (>100 individuals) were always dense, whilst smaller flocks were somewhat less compressed (Fig. 4, shown for social flocks only; there was a negative relationship between (log-transformed) nearest neighbor distance and (log-transformed) flock size,  $F_{1,21} = 65.2$ ,  $P < 0.001$ ).

Social foraging was recorded both diurnally and nocturnally (Fig. 5). The only reliable data on the occurrence of social feeding were between 05.00 h and 18.00 h, after which little success was had in making observations due to the limitations of the night-vision equipment. Figure 5 does not illustrate well the impression we got from being in the field—that social foraging is probably much more prominent at night than at day and for some species (e.g., Avocet, White Pelican) social feeding at night may provide the bulk of their food intake. Nevertheless, Figure 5 does show that social feeding occurred

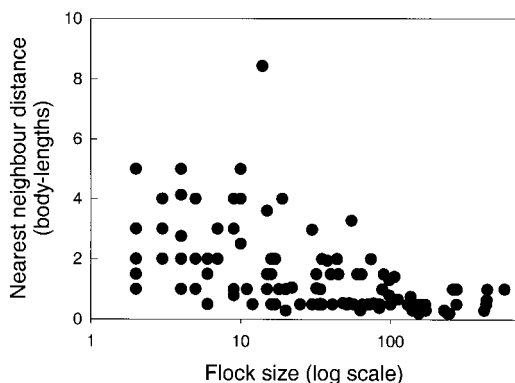


Figure 4. Nearest neighbor distance plotted against feeding flock size for social flocks in Songor and Keta Lagoons in October and November 1994.  $N = 122$  flocks. Note the logarithmic x-axis.

throughout the daylight period, but was most pronounced in the late afternoon. Another peak occurred in the middle of the night.

#### Correlates with diet

From observations of feeding techniques and observed intakes, it was clear that small tilapia were the main prey being taken in social feeding flocks. Fish-eaters constituted the vast majority of the social feeders in flocks (Table 1:  $\chi^2_1 = 84.9$ ,  $P < 0.001$ ). Guilds

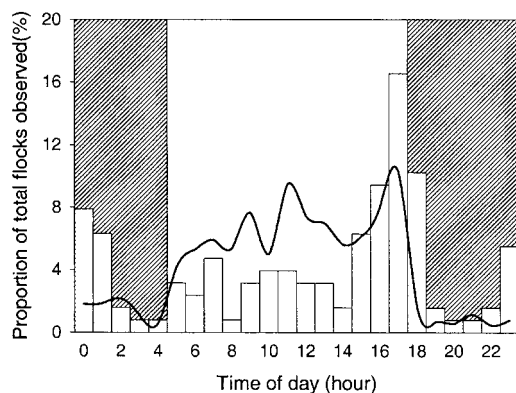


Figure 5. Time of occurrence of social and non-social foraging flocks in Songor and Keta Lagoons in October and November 1994. The hatched area represents the period of darkness, during which observations were not very successful compared with during daylight. Occurrence of flocks is expressed as a percentage of the total number of flocks observed. Bars represent social flocks; the line represents non-social flocks.  $N = 127$  social flocks and 2,422 non-social flocks.

also differed in their contribution to the proportion of flocks that were social ( $\chi^2_4 = 9.5$ ,  $P < 0.001$ ). Among the fish-eating species, the *Tringa* shorebirds and Avocet showed the highest incidences of social foraging. Thus, while the main guilds and species involved in socially foraging flocks were largely or wholly piscivorous, the larger sandpipers made up a disproportionate share of the social feeding component.

#### Prey availability

No robust measures of fish density were made at Keta, due to variation in selectivity and presumed efficiency of the three fishing methods we tried, and no attempts were made at Songor. A sweep net (based on local design, consisting of three m of 1-mm mesh polythene mosquito net strung between two broomsticks, operated by two people) caught small fish (mainly 0.5-1.5 cm length) at Fiahor and Tegbi. These fish are probably important prey for socially feeding waders. Density estimates ranged from 0.72-2.26 individuals/m<sup>2</sup>, although these are almost certainly underestimates due to the ability of fish to escape the net. Visual observations of tilapia of this size herded by researchers suggested local densities easily reached 100/m<sup>2</sup>. Small tilapia are apparently highly patchy in their distribution. Naturally or artificially enhanced densities (e.g., schools) could be important temporary food sources.

#### DISCUSSION

Social foraging was a widespread phenomenon in the shallow coastal lagoons of Ghana during this study, especially within the long-legged (mainly *Tringa*) waders. Over half of the Marsh Sandpipers and over a third of the feeding Greenshanks, Spotted Redshanks and Avocets that we recorded foraging, fed in social flocks. While social foraging was recorded in White Pelicans just once during this study, this was largely because pelicans were concentrated into a single flock on a very large lagoon (Keta) and were seldom encountered. Their behavior (roosting on dry mudflats until just before dusk

then all feeding in a single flock; flying at dawn from wet regions towards the dry roosting area at Fiahor) suggests that nocturnal or crepuscular social feeding is common in these pelicans.

Social foraging flocks were typically larger and denser than non-social flocks (Figs 2 and 3), and primarily (probably entirely) involved fish-eating birds. A plowing line of birds probably herds fish together, temporarily increasing prey availability. By walking in a line, we were able to herd schools of very small tilapia for some distance, especially by blocking their escape reactions to the sides, and local people fish in this fashion. A line of plowing birds probably maintains fish densities far above that which a solitary feeding bird would encounter.

The running of plowing waders in flocks during daylight is presumably an attempt to overtake fish attempting to escape. This seemed to be a very successful feeding technique, judging by the few occasions when we were able to follow an individual bird. A feeding run by a *Tringa* wader typically lasted only several seconds but could cover 5-20 m in this time, and the bird could be seen making several swallows (presumed fish captures). The predominance of plowing at night may reflect the relative benefit of tactile foraging compared with visual foraging (pecking). Plowing was frequently seen in breakaway groups from pecking flocks, presumably because it requires open water for the running birds. Foraging success of Spoonbills in The Netherlands is affected by position in flocks (Voslamber and Buijse 1996), and this is likely to be true for socially feeding shorebirds. Aggressive interactions were noted between individuals at the front of social flocks, suggesting that there is competition for the "front line" of the foraging flock. However, a high intake rate was not exclusive to synchronous behavior. Large, dense, pecking assemblages also had apparently high feeding rates.

Many studies of herons and egrets have shown that individuals join aggregations based on the presence of other birds (e.g., Kushlan 1977; Caldwell 1981; Erwin *et al.* 1985; Smith 1985). This "local enhance-

ment" relies on the presence of feeding individuals or species (especially Snowy Egrets (*Egretta thula*) in the western hemisphere: Kushlan 1977; Caldwell 1981) that signal good resource levels (although this is not always so: see Alonso *et al.* 1994).

Social flocks in Ghana apparently do experience high prey availability. Terns, especially Little Terns (*Sterna albifrons*), were often seen diving in and around social flocks, indicating abundant food. We have no data on prey levels before the formation of social foraging flocks or during their persistence, so we cannot test whether flocks merely form at existing prey "hot-spots", or whether social flocks create or prolong artificially high prey densities. We suspect that (as Boettcher *et al.* 1994 suggest for American Avocets feeding on nektonic invertebrates) social flocks actively enhance prey availability through the presence and actions of many individuals. This is easy to envisage in synchronized "sweeping" lines of birds, but even the dense pecking assemblages must obstruct the escape attempts by fish. These pecking flocks may not necessarily have started socially; they could simply have formed in an area of high prey density (e.g., in weed beds), in which case scramble competition might best describe the behavior. The persistence of these pecking flocks, however, probably is a social effect (albeit indirect) in which escape reactions of fish become confused through the presence of large numbers of birds. If socially feeding waterbirds do concentrate prey for the terns mentioned above, then this provides a nice parallel to marine situations in which predatory fish force smaller fish to the surface of the sea, making them available to terns (Safina and Burger 1989).

Social flocks were notable for their noise; on a calm day they could be heard from 500 m or more away, and at night, while we were largely unable to see flocks, the noise was considerable. The feeding vocalizations of these flocks may bring more birds in to the flock, and so enhance or prolong the feeding (rather than communicate that "all is well" in regard to predators; Kushlan 1976).

The large majority of social foraging in this study was done by the *Tringa* shorebirds.

These species feed on small fish, and interference or stealing was not recorded. Intake rates within these assemblages could be high enough that stealing would not be beneficial. Alternatively, the small size of the prey might make the prey capture event too fast to allow any form of kleptoparasitism (c.f. Ens *et al.* 1990). Interference was noted occasionally in the egrets and herons, possibly because their larger prey size necessitated a longer handling time, with more opportunities for stealing.

Social feeding is a common and widespread feeding method in several species of birds in coastal Ghanaian wetlands. It probably contributes considerably to the energy intake of many species each day, and may provide almost all the energy for one (White Pelican). In contrast, social feeding appears to be uncommon in waders in Europe, even in the same species (Avocet and Spotted Redshank do feed in flocks in muddy gullies in the Wadden Sea, but Greenshank and Redshank only rarely: pers. obs.). Understanding the functional significance of this social behavior depends on comparing the foraging success and the energy budgets of social and solitary feeders, both within and between species. It will be important to separate any site effects (e.g., prey availability, water depth) from those of the birds themselves (e.g. diet, condition, reproductive state). While this is a challenging task, studying the roles of these distinctive social foraging elements in creating or maintaining temporary patches of high prey availability would determine how direct the effects of social flocks on food availability are. The situation with socially feeding waterbirds parallels that of seabirds, where the presence of multi-species feeding associations is identified as common and prominent, but their dynamics and importance in seabird ecology is only now being elucidated (Camphuysen and Webb 1999).

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