

# FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

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**ABSTRACT:** Great Egrets (*Ardea alba*) foraging in grassy uplands near Arcata, California, used multiple strategies, foraging solitarily or in groups and commensally or noncommensally, in any of the four possible combinations. Egrets foraging commensally with cattle apparently benefited from the association on eight of the 21 observed occasions. Solitary foragers tended to use microhabitats along ditches and fences and were generally less active, made fewer errors, and captured larger prey than did group and commensal foragers. But group foragers, commensal and noncommensal foragers combined, captured more prey. Tidal fluctuations, prey types, and habitat structures likely modified foraging behaviors. There was no clear difference in rate of food intake, handling time, or foraging success by foraging strategy: a higher rate of capture of small prey by egrets foraging in groups compensated for the lower rate of capture of larger prey by solitary birds.

The Great Egret (*Ardea alba*) is commonly associated with wetlands but also forages in uplands, occasionally commensally with grazing mammals (Caldwell 1956, Kushlan 1978b, Herring and Herring 2007) and in aggregations with others of its species (Kushlan 1978a, Wiggins 1991). In northern California's Humboldt Bay, Great Egrets nest colonially on islands within the bay and often fly to the nearby mainland to feed (Ives 1972). Humboldt Bay was historically surrounded by freshwater marshes, but 95% of these were diked and drained for agriculture in the late 1800s and early 1900s (Long and Ralph 2001). These agricultural areas contain rich sources of food for foraging egrets (Schlorff 1978). Given that food is a limiting factor for predatory birds (Lack 1946) and that individuals may vary in their ability to exploit resources (Reid et al. 2003), different behaviors may return better results in different habitats (Kushlan 1972, 1976, Maccarone and Brzorad 2007). The Great Egret's feeding behavior, aggression, and sociality may be expressed and interact differently in different habitats (Kushlan and Hancock 2005). Interspecific and intraspecific interactions may contribute to the Great Egret's various feeding behaviors (Kushlan 1976).

The goal of my study was to compare the Great Egret's behaviors and success when foraging in groups of various sizes and commensally or noncommensally in upland habitats. I aimed to identify functions of the Great Egret's social system and how various habitats contribute to the species' ecology.

## METHODS

### Study Area

My study took place in an area of ~2415 ha in the Arcata Bottoms (40.9° N, 124.1° W) north of Humboldt Bay, Humboldt Co., California, from 25 January to 27 March 2010. The upland landscape consists of pastures for dairy and beef cattle (Monroe 1973). The fields ( $n = 92$ ) vary in size, shape,

and composition and are separated by roads, ditches, fences. They are vegetated with ryegrass (*Lolium perenne*), dandelion (*Taraxacum officinale*), plantain (*Plantago lanceolata*), velvet grass (*Holcus lanatus*), Kentucky bluegrass (*Poa pratensis*), meadow fescue (*Festuca arundinacea*), bentgrass (*Agrostis* spp.), clover (*Trifolium* spp.), and buttercup (*Ranunculus repens*) (Black et al. 2003). The Arcata area receives 1000–1300 mm of rainfall annually, mainly in winter and spring, and it may be foggy year round. Temperatures seldom dip below  $-1^{\circ}\text{C}$  in winter and rarely climb above  $21^{\circ}\text{C}$  in summer. Tidal sloughs connected to Humboldt Bay wind through the study area and are used for irrigation. Consequently, some upland areas had characteristics of wetlands, being variably saturated and supporting mainly hydrophytic plants. As my study focused on the egret's use of uplands, I excluded observations in wetlands.

### Foraging Behaviors and Interactions

For this study I defined “foraging” as an egret standing, pacing, or probing with its head and bill down. “Feeding” was a successful strike, capture, and swallowing of prey. I defined foraging strategies as “solitary” (individual  $>10$  m from another Great Egret or other species) or “grouped” (individual  $\leq 10$  m from another Great Egret or other species). I categorized the size of a group as 2–15, 16–30, or  $\geq 31$  egrets and identified foraging as commensal or noncommensal. Egrets foraging both noncommensally and commensally could be feeding either solitarily or in groups. “Commensal foraging” consists of one species inadvertently displacing potential food items, making them available to an “attendant” species, thus aiding the attendant's foraging while receiving no benefits and paying no cost (Wiens 1989). I identified commensal foraging of a Great Egret by its following, in the same direction, at a similar pace, and at a distance  $<2$  m, another animal such as a grazing cow.

After selecting a specific egret (“focal animal sampling,” Altmann 1974) for observation, I recorded its foraging behavior for 20 minutes or until it left the habitat. During these observations, through a spotting scope, I recorded the number of birds present, capture tactics (e.g., neck wobble, stand and wait, bill clapping, fast/slow walk; see Krebs 1974, Kushlan 1976, Kelly et al. 2003), prey type, prey size (in relation to the bill; Bayer 1985), steps, “errors” (drops, a strike at an item other than prey, or an unsuccessful strike), time spent handling prey, probes (moving debris with the bill without striking), strikes, and captures. I also noted interference with foraging such as conspecific aggression when another bird was  $<5$  m from a foraging egret or when another individual flew into a field with a solitary egret. “Aggression” consisted of an egret raising its feathers, chasing another bird, attempting kleptoparasitism, or engaging in combat, displacing the other bird. I excluded the time such a bird was in flight from the observation time. “Relocations” consisted of a bird moving from one location to another within the same field and continuing foraging. Before and after sampling I recorded the presence of other animals and sources of disturbance (e.g., loud noise, motor vehicles, or human interference) that noticeably altered an egret's behavior.

To randomize sampling, I randomized observations by time of day, spread observations among the various agricultural habitats, observed foraging birds

## FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

at randomly selected sites within a habitat, and chose only one bird per site for focal observation, limited to birds close enough for me to identify their food, generally <100 m. I ensured that timed observations were independent and avoided repeated sampling of individuals and groups by moving to a different location for each observation. In cases where my arrival disturbed a foraging egret noticeably, I allowed it 1–20 minutes to adjust. If weather such as high wind, fog, heat distortion, or rain impaired the accuracy of an observation, I terminated it. For each 20-min observation, I recorded the time, tide (as flood or ebb and as low or high), wind speed, wind direction, percent cloud cover, and precipitation (<http://www.noaa.gov/wx.html>).

### Diet

Possible prey items, which I assumed to be similar across the habitats sampled, included earthworms, the Northern Red-legged Frog (*Rana aurora*), Pacific Treefrog (*Pseudacris regilla*), and voles (*Microtus* spp.). I left an item unidentified if it was captured and ingested in <1 sec. From the size of an item, I estimated its biomass on the basis of Siegfried (1969), Ricklefs (1974), and Schlorff (1978), and from these estimates I calculated intake rates (g/min), total energy content (kcal/g wet mass), and total energy content per individual (kcal). With reference to the average exposed culmen of 12 specimens of the Great Egret at Humboldt State University (109.1 mm, sexes combined), I categorized prey as small ( $\leq 1/4$  bill length or  $\leq 27$  mm), medium ( $1/4$ – $3/4$  bill length or 28–81 mm), or large ( $> 3/4$  bill length or  $\geq 82$  mm).

### Habitat Characteristics

The habitats surveyed varied in vegetation height, providing prey with a varying degree of cover. Adapting the method of Burger and Gochfeld (1993), I categorized the height of vegetation in comparison to the length of a foraging bird's tarsus (mean 148.2 mm, sexes combined; Herring et al. 2008) as short ( $< 1/3$  tarsal length or  $< 50$  mm), medium ( $1/3$ – $2/3$  tarsal length or 50–75 mm) and tall ( $\geq 2/3$  tarsal length or  $> 75$  mm).

### Statistical Analysis

I expressed the rates of strikes, errors, captures, pace, and probes per minute over a 20-min observation period and capture success as the number of successful captures divided by the total number of strikes. Using SAS, version 9.1.3, I calculated Pearson correlation coefficients between total time foraging, strike rates, probe rates, error rates, capture rates, and capture success to test correlation strengths. I defined highly correlated measures as those with the absolute value of  $r > 0.40$  and  $P < 0.0001$ . To estimate the effect of foraging strategies (commensal or not, group or solitary, and interaction), I ran a multivariate analysis of covariance on correlated measures and analysis of covariance on uncorrelated measures, with observation time and flock size as covariables. I estimated least-squares means and standard errors (SE) for these comparisons and in all analyses set the threshold of significance at  $\alpha = 0.01$ .

## RESULTS

## Foraging Behaviors and Success

I observed foraging egrets in 123 sessions over the 52 days of sampling, totaling 2069 min. The average length of an observation was 16.82 min (SE = 0.50), range 2–20 min. Groups contained up to 80 birds. I observed solitary noncommensal egrets ( $n = 50$ ) for a total of 826.37 min ( $16.53 \pm 0.89$ ) and group-foraging noncommensal egrets ( $n = 44$ ) for a total of 723.26 min ( $16.44 \pm 0.89$ ). For egrets foraging commensally these times were 143.00 min ( $15.89 \pm 1.88$ ) for solitary egrets ( $n = 9$ ) and 376.31 min ( $18.82 \pm 0.86$ ) for group-foraging egrets ( $n = 20$ ). Egrets foraged in association with solitary cows and herds of up to 84. Of the 29 instances of commensal foraging, 21 were with cattle, four were with gulls, and four were with Aleutian Cackling Geese (*Branta hutchinsii leucopareia*). Commensal foragers received apparent rewards on eight occasions of foraging with cattle (38%), one occasion with gulls (25%), and on three occasions with Aleutian Cackling Geese (75%).

During the 123 observations, I noted 18 instances of aggression between egrets foraging noncommensally (15%). Of these, 7 involved groups, 11, solitary birds. Among egrets foraging commensally, I noted conspecific aggression on only two occasions, once from a solitary bird and once in a flock of 12 birds. Conspecific aggression included chases on foot (16 instances), flight chases (one instance), and attempted kleptoparasitism (one instance). Flights and relocations were observed a total of 114 times. Egrets foraging in groups, whether they were foraging commensally (0.16 times per minute,  $\pm 0.09$  SE) or noncommensally ( $0.16 \pm 0.06$ ), relocated more often than did solitary egrets ( $0.07 \pm 0.13$  and  $0.06 \pm 0.06$ , respectively). But the difference was not statistically significant.

Table 1 summarizes measures of foraging effort and success. Pearson correlations confirmed strong associations among strike rate, pace rate, error

**Table 1** Measures of Foraging of Great Egrets in Uplands of the Arcata Bottoms, Humboldt Co., California, 25 January–27 March 2010<sup>a</sup>

Metric	Noncommensal		Commensal	
	Solitary	Grouped	Solitary	Grouped
<i>n</i>	50	44	9	20
Total time foraging (min)	48.0 $\pm$ 8.0	51.1 $\pm$ 8.5	77.0 $\pm$ 18.1	67.2 $\pm$ 12.3
Strike rate (per min)	0.31 $\pm$ 1.78	5.30 $\pm$ 1.88	0.32 $\pm$ 4.00	2.46 $\pm$ 2.73
Probe rate (per min)	0.01 $\pm$ 0.39	1.09 $\pm$ 0.41	0.00 $\pm$ 0.88	0.41 $\pm$ 0.60
Pace rate (per min)	2.60 $\pm$ 7.81	23.88 $\pm$ 8.23	3.14 $\pm$ 17.53	13.55 $\pm$ 11.96
Error rate (per min)	0.04 $\pm$ 0.11	0.28 $\pm$ 0.12	0.05 $\pm$ 0.25	0.22 $\pm$ 0.17
Capture rate (per min)	0.24 $\pm$ 1.68	5.02 $\pm$ 1.77	0.28 $\pm$ 3.77	2.28 $\pm$ 2.57
Relocation rate (per min)	0.06 $\pm$ 0.06	0.16 $\pm$ 0.06	0.07 $\pm$ 0.13	0.16 $\pm$ 0.09
Intake rate (g/min)	0.87 $\pm$ 0.12	0.55 $\pm$ 0.13	0.55 $\pm$ 0.27	0.99 $\pm$ 0.18
Handling time (sec)	22.3 $\pm$ 4.6	6.8 $\pm$ 4.9	9.2 $\pm$ 10.4	4.8 $\pm$ 7.1
Foraging success (%)	94 $\pm$ 2	96 $\pm$ 2	95 $\pm$ 4	93 $\pm$ 3

<sup>a</sup>Values are least-square means  $\pm$  standard error.

## FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

rate, and capture rate (all values  $>0.9$ ). Correlations of these measures with relocation rate, handling time, prey-intake rates, capture success, and total time foraging were weaker to none. Wilks' lambda ( $\Lambda$ ) from multivariate analysis of covariance indicated no overall difference between commensal and noncommensal foraging ( $\Lambda = 0.97$ ,  $F = 0.71$ ,  $P = 0.62$ ) and none between solitary and group foraging ( $\Lambda = 0.97$ ,  $F = 0.63$ ,  $P = 0.68$ ). In addition, there was no interaction between whether or not foraging was commensal and whether or not it was in a group ( $\Lambda = 0.98$ ,  $F = 0.37$ ,  $P = 0.87$ ). The covariates of flock size ( $\Lambda = 0.89$ ,  $F = 2.83$ ,  $P = 0.02$ ) and observation time ( $\Lambda = 0.92$ ,  $F = 2.02$ ,  $P = 0.08$ ) were not significant. Furthermore, there was no difference by strategy in rates of error ( $P = 0.27$ ), strike ( $P = 0.22$ ), probe ( $P = 0.22$ ), pace ( $P = 0.22$ ), or capture ( $P = 0.22$ ). Neither was there any difference by strategy in relocation rate ( $F_{1,117} = 1.0$ ,  $P = 0.32$ ), capture success ( $F_{1,117} = 1.24$ ,  $P = 0.30$ ), or total time foraging ( $F_{1,117} = 0.06$ ,  $P = 0.80$ ). For egrets in flocks, flock size had no effect on capture success ( $F_{3,114} = 1.15$ ,  $P = 0.14$ ). Mean success by three categories of flock size was  $95.5 \pm 1.9\%$  for 2–15 birds,  $87.4 \pm 3.4\%$  for 16–30 birds, and  $90.6 \pm 5.3\%$  for 31–84 birds.

The capture rate of grouped foragers was 10 to 20 $\times$  the rate of solitary foragers, a significant difference (multivariate analysis of variance,  $P = 0.005$ ). Yet the intake rate (g/min) differed by a factor of less than 2, and among noncommensal foragers the intake rate of solitary foragers was greater even though their capture rate was only 5% that of the grouped foragers. So the few voles caught by the solitary foragers more than made up for all the earthworms and frogs caught by the grouped foragers.

### Diet

By number of prey items, the diet of solitary commensal foragers consisted 54% of invertebrates (mainly earthworms), 11% of frogs, 1.5% of voles, and 34% unidentified. The diet of Great Egrets foraging commensally in a group was 55% invertebrates, 7% frogs, 0% voles, and 38% unidentified. Of egrets foraging noncommensally, the diet of those in flocks was 61% invertebrates, 7% frogs, 0.1% voles, and 33% unidentified, while that of solitary foragers was 33% frogs, 25% earthworms, 4% voles, and 38% unidentified. The voles, up to 10 cm long and 28 g in weight, were rich sources of energy. I noted 13 captured by solitary foragers but only one by group foragers (Table 2). Both strategies combined, group foragers captured more total prey ( $F_{1,118} = 21.99$ ,  $P < 0.001$ ) (Table 2). Solitary and grouped foragers did not differ in mean time handling prey ( $P = 0.94$ ) or mean intake rate ( $P = 0.76$ ).

### Habitat Characteristics

Usage of vegetation heights differed by foraging strategy ( $\chi^2_6 = 19.48$ ,  $P = 0.003$ ). Solitary foragers used taller vegetation more frequently (40/50 instances or 80%) than did group foragers (20/44 instances or 45%). Solitary egrets feeding commensally were mainly in tall vegetation (7/9 instances or 78%), whereas groups feeding commensally used vegetation heights nearly evenly (50% short, 45% tall). The difference between commensal and noncommensal foragers in use of upland habitat by tide level was nearly

FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

**Table 2** Numbers of Prey Captured by Great Egrets near Arcata, California, 25 January–27 March 2010, by Type, Size, and Mode of Foraging

Mode and prey	n <sup>a</sup>	Size			Total	Percent
		≤27 mm	28–81 mm	≥82 mm		
Noncommensal solitary	50					
Earthworms		28	25	20	72	25%
Frogs		42	53	0	95	33%
Voles		0	1	11	12	4%
Unidentified		99	9	0	108	38%
Noncommensal grouped	40					
Earthworms		396	109	101	606	61%
Frogs		36	30	0	66	7%
Voles		0	0	1	1	0.1%
Unidentified		323	3	0	326	33%
Commensal solitary	9					
Earthworms		27	8	0	35	54%
Frogs		4	3	0	7	11%
Voles		0	0	1	1	1.5%
Unidentified		21	1	0	22	34%
Commensal grouped	20					
Earthworms		261	90	46	397	55%
Frogs		40	8	0	48	7%
Voles		0	0	0	0	0%
Unidentified		276	1	0	277	38%

<sup>a</sup>Number of egrets observed, for up to 20 min per individual.

significant ( $\chi^2_3 = 10.03, P = 0.018$ ). Commensal foragers used upland areas more often at low tide (total of 17/29 instances or 59%, grouped and solitary foragers combined), while noncommensal foragers tended to prefer high tide (total of 67/94 instances or 71%, grouped and solitary foragers combined). Over the study, foraging egrets were associated with characteristics of wetland habitat 22% of the time.

DISCUSSION

While foraging, Great Egrets often gathered into groups of various sizes, and they arrived and departed feeding sites more or less simultaneously. Krebs (1974) proposed that birds nesting colonially may follow one another to discover food sources. Birds may also be attracted to feeding areas by seeing another feeding (Poysa 1992). The egrets I studied likely exploited these strategies. Interactions such as competition and aggression that arise during foraging in a group likely make group foraging more costly (Goss-Custard and Durell 1987). Of the egrets I observed, group foragers did suffer a greater rate of striking errors, which were possibly the result of increased competition. But group foraging also enhances the mean rate of food intake (Beauchamp 1998) by decreasing the time each individual must devote to vigilance (Sullivan 1984), enabling herding of mobile prey (Swynnerton 1915), and allowing imitation of behaviors of other individuals

(Krebs 1973, Morse 1978). Because of the large number of unidentified prey, I did not evaluate the data on energy intake. Therefore, my results may not reflect differences in how the birds managed their time or achieved energy balance. But I found no detectable differences in mean intake rate by foraging strategy, possibly because food was abundant in the habitats I surveyed. Beauchamp (1998) proposed that the rate of food intake increases when resources are more concentrated in space and that food dispersal may influence group size. Gawlik (2002) suggested that Great Egrets typically remain at a site until they deplete the prey. So the birds I observed likely switched tactics as needed to increase intake rates and success.

Solitary egrets foraging along fence rows and ditches defended their space more than did group foragers. Thus solitary foragers suffered costs from displacement and aggression. Prey are likely larger, more concentrated, or more available along fence rows and ditches prey than in the open fields in which groups foraged. As a result, egrets could defend these areas, precluding groups from forming. Attempts to capture large prey occasionally entailed the increased effort of capture in flight, by diving, by fast running, extended handling times, and long periods of stalking or waiting. On average, birds that were less active (i.e., solitary foragers) took prey larger than that taken by group and commensal foragers, possibly because of the lack of competition.

By displacing prey and disturbing the substrate, cattle made prey more available to egrets following them. Though published reports of Great Egrets foraging commensally with mammals are few (Dean and MacDonald 1981, Ruggiero and Eves 1998, Herring and Herring 2007), this behavior may increase foraging success (Kushlan 1978b), as it does for the Cattle Egret (*Bubulcus ibis*) (Heatwole 1965, Dinsmore 1973 and Grubb 1976). Burger and Gochfield (1982) found that in the Cattle Egret selectiveness for a mammal ("host") and availability of prey are positively correlated; the egret forages in the way that maximizes efficiency. In my study I could not ascertain selectiveness for a host. The assumption that prey captured by commensal foragers was a direct "reward" of associating with other birds or cattle may not be fully justified. Rather, solitary egrets foraging noncommensally may have been trying to discourage the competition from another bird. In contrast, when feeding primarily with grazing cattle, a solitary egret would have no added competitive pressure and thus receive unrestricted benefit from cattle flushing prey.

Behavioral plasticity may have improved foraging success. The Great Egrets I studied often modified their behavior as they shifted among microhabitats differing in prey and vegetation height. Characteristics of a wetland and level of the tide contribute to plasticity of foraging (Erwin et al. 2006). Although the risk of predation may have influenced the egrets' foraging behavior, that risk was presumably low across the study area. Despite different behaviors used to capture prey, the rate of success of all strategies was similar (Table 1). Two different strategies, solitary foraging that occasionally yielded a few large prey and grouped foraging that frequently yielded many small prey, gave similar returns, and the egrets had the behavioral plasticity to pursue either.

Great Egrets often behaved socially, competing, interacting aggressively or territorially, forming groups, and arriving and departing feeding sites at the

## FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

same general time. Sexual, age, genetic, and environmental differences may all contribute to the Great Egret's diversity of behaviors (Lott 1984). Since I had no data on the egrets' sexes, ages, or genetics, these factors likely biased the results. Lott (1984) proposed several possible sources of such variation: experience (including learning during a critical period), imitation, culture, classical conditioning, demography, niche breadth, environmental stability, social system, psychological complexity, and hormones. The observed behavioral variation could be caused by frequency-dependent selection or selection for an adaptive plasticity that permits individuals to adjust their behavior in response to abiotic variables (Lott 1984). Given my results, I hypothesize that the Great Egret's social system varies intraspecifically. Such variation could be adaptive (Eisenberg 1966), relevant to attempt to manage or predict changes in a species' social system.

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## FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

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## FORAGING INTERACTIONS OF THE GREAT EGRET IN UPLAND HABITATS

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Great Egret

Sketch by Narca Moore-Craig