GROUP-FORAGING EFFECTS ON CAPTURE RATE IN WADING BIRDS

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Abstract. Group foraging is common among wading birds, and the reasons why individuals forage in groups are of theoretical and practical interest. Although aggregations of foraging wading birds usually form within patches of high-quality habitat, individual wading birds can sometimes increase success by foraging near others. We investigated the hypothesis that individuals derive a benefit from foraging in groups separate from benefits due to habitat quality. We measured the capture rates of birds foraging solitarily and in groups at foraging sites and paired unused sites and used generalized linear mixed models and information-theoretic model selection to access the evidence that individuals increase their foraging success when foraging in groups. The capture rate of Great Egrets (*Ardea alba*) in groups was higher, supporting the hypothesis that individuals benefit from the presence of other foragers. This rate was highest in intermediate-sized groups but tapered off in larger groups, suggesting that interference competition limits success. Tricolored Herons (*Egretta tricolor*) showed a similar but less statistically precise pattern. Contrary to expectation, the capture rate of Snowy Egrets (*E. thula*) foraging alone was higher than that of those in groups. Although fish abundance was greater at used than at unused sites, and at sites with groups than at sites with individuals, we did not detect an effect of prey density on capture rate, probably because prey density was fairly high at all sites studied. Our study adds to the evidence for a direct benefit to individuals due to the presence of other foragers in aggregations.

Key words: aggregation, foraging success, Great Egret, group foraging, Snowy Egret, social-facilitation hypothesis, Tricolored Heron.

Efectos del Forrajeo en Grupo sobre la Tasa de Captura en Aves Vadeadoras

Resumen. El forrajeo en grupo es común entre las aves vadeadoras y las razones por la que los individuos forrajean en grupo son de interés teórico y práctico. Aunque las agregaciones de forrajeo de aves vadeadoras usualmente se forman adentro de parches de hábitat de alta calidad, las aves vadeadoras individuales pueden a veces incrementar su éxito forrajeando cerca de otras. Investigamos la hipótesis de que los individuos obtienen un beneficio de forrajear en grupos distinto de los beneficios atribuidos a la calidad del hábitat. Medimos las tasas de captura de aves forrajeando de forma solitaria y en grupos en sitios de forrajeo y sitios pareados no usados, y empleamos modelos mixtos lineales generalizados y selección de modelos basados en la teoría de la información para evaluar la evidencia de que los individuos aumentan su éxito de forrajeo cuando forrajean en grupos. La tasa de captura de *Ardea alba* en grupos fue mayor, apoyando la hipótesis de que los individuos se benefician de la presencia de otros individuos forrajeando. Esta tasa fue más alta en grupos de tamaño intermedio pero desapareció en grupos mayores, sugiriendo que la competencia por interferencia limita el éxito. *Egretta tricolor* mostró un patrón similar pero estadísticamente menos preciso. Al contrario de lo que se espera, la tasa de captura de individuos de *E. thula* forrajeando solos fue mayor que la de aquellos en grupos. Aunque la abundancia de peces fue mayor en los sitios usados que en los no usados y en los sitios con grupos que en los sitios con individuos, no detectamos un efecto de la densidad de presas en la tasa de captura, probablemente porque la densidad de presas fue bastante alta en todos los sitios estudiados. Nuestro estudio aporta evidencia a la existencia de un beneficio directo para los individuos por la presencia de otros individuos forrajeando en forma agregada.

INTRODUCTION

Aggregations of foragers are a conspicuous phenomenon that occurs in a variety of animals (Krause and Ruxton 2002), including wading birds (e.g., Erwin 1983b, Kersten et al. 1991, Master et al. 1993). Several hypotheses have been proposed to explain how individuals benefit from foraging in mixed-species aggregations. These can be summarized in four broad categories: attraction of individuals to high-quality patches (Fretwell

and Lucas 1970), protection from predators (Hamilton 1971), information exchange among individuals (Valone and Giraldeau 1993, Dall et al. 2005), and direct enhancement of individuals' foraging success due to the presence of other foragers (social facilitation; Kushlan 1978b). These hypotheses are not mutually exclusive, and more than one might be operating at any given time (Morse 1970, Powell 1985). In this paper we focus on the distinction between benefits to individuals due to patch quality versus benefits due to the presence of other foragers.

Examples of some ways that each of these categories might apply to wading birds foraging in aggregations will help clarify these distinctions. For example, there is ample evidence that mixed-species aggregations of wading birds often form in areas of high prey density (Kushlan 1976b, Erwin et al. 1985, Smith 1995). Other studies have shown that wading birds locate patches of prey by using the presence of other foragers; this is often referred to as local enhancement (Krebs 1974, Kushlan 1976a, Caldwell 1981, Erwin 1983b). Similarly, the risk of predation to members of a foraging flock might be reduced through increased predator detection, predator confusion and risk spreading (Hamilton 1971, Yaukey 1995, Larsen 1996); such a benefit has been shown for wading birds (Caldwell 1986). Less time devoted to vigilance can also lead directly to increased foraging success if an individual feeding in an aggregation can spend more time foraging (e.g., Caraco 1979, Elger 1989, Hino 1998).

Foraging success might also be improved through gaining additional information about the location of prey within a patch (Valone 1989, Valone and Giraldeau 1993), or learning from other foragers about foraging tactics, or novel prey types (Krebs and Inman 1992, Beauchamp et al. 1997). For example, some species of wading birds may act as focal or core members that attract others to mixed-species foraging aggregations (Kushlan 1977, Smith 1995, Strong et al. 1997). Caldwell (1981) showed that the proximity to Snowy Egrets (*Egretta thula*) was positively correlated with foraging success for Great Egrets (Ardea alba), Tricolored Herons (*E. tricolor*), and Little Blue Herons (*E. caerulea*).

If prey is mobile and cryptic, the physical presence of foragers might disturb prey, making it more susceptible to predation and thereby improving individuals' foraging success (Morse 1970, Rodrigues et al. 1994, Hino 1998). It is plausible that this mechanism might apply to wading birds feeding on schooling fish. Neill and Cullen (1974) have shown that individual fish isolated from schools may become more susceptible to predators. Smith (1995) noted that wading birds feeding on schooling fish can cause the schools to become confused, and Kushlan (1978a) demonstrated that Little Blue Herons increase their foraging success rate in this way when foraging near White Ibis (*Eudocimus albus*). This is often referred to as the beating effect, but social facilitation is perhaps a better term because it does not imply the mechanism by which an individual benefits from the presence of other foragers.

These examples illustrate how various ecological factors may affect wading birds' foraging success and underscore the challenge of differentiating between enhanced foraging success due to foraging in better patches of prey versus that due to the presence of other foragers. Attention to this topic is warranted because mixed-species foraging aggregations are a prominent feature of wading birds' foraging ecology (Gawlik 2002, Stolen et al. 2007), and wading birds are an important component of many systems, (Crozier and Gawlik 2003, Stolen et al. 2005). Although many studies have evaluated this question, only three (Krebs 1974, Master et al. 1993 and Erwin et al. 1985) have measured levels of prey density, the presumed underlying factor governing the tradeoffs between solitary and group foraging strategies. Of the three studies, only Master et al. (1993) assessed the tradeoffs between solitary and group foraging for the Snowy, Tricolored and Great Egrets, the species of interest in our study. Results of this study are of broader interest because while examples of foragers using other group members as a source of public information are emerging rapidly (Danchin et al. 2004, Valone and Templeton 2002), few have considered the direct benefit of other group members on foraging success. Demonstration of this effect in wading birds would point out an important benefit of membership in a foraging group, which researchers should consider in all taxa engaging in group foraging. The results may generalize to other species that forage for mobile cryptic prey susceptible to disturbance such as insectivorous passerines, pelagic birds, waterfowl, gulls, and terns.

We studied the rate of foraging success for three species of piscivorous wading birds foraging alone and in groups. To isolate the effect on foraging success due to patch quality versus that due to the presence of other foragers, we measured the prey density and habitat characteristics at the sites. We focused on three questions about the effects of prey density and foraging-aggregation size on foraging success: (1) do wading birds select foraging sites with prey density or biomass greater than at nearby unused sites, (2) do foraging aggregations of wading birds occur at sites with prey density higher than at sites occupied by individuals, and (3) what is the relative importance of prey density and the presence of other foragers on foraging success (i.e., is there evidence for the social-facilitation hypothesis)?

METHODS

STUDY SITE

Our study site consisted of areas of impounded salt marsh in the 55 000-ha Kennedy Space Center/Merritt Island National Wildlife Refuge (hereafter KSC/MINWR). This site is located in the northern portion of the Indian River Lagoon system, a subtropical estuary that is an important site for wading birds on the southeastern Atlantic coast of North America (Breininger and Smith 1990, Schikorr and Swain 1995, Sewell et al. 1995, Smith and Breininger 1995, Stolen et al. 2002). Mixed-species foraging aggregations of several hundred or more individuals are common in impounded wetlands at KSC/MINWR (Stolen 2006, Stolen et al. 2007). Because of the linear nature of the Indian River Lagoon system, this
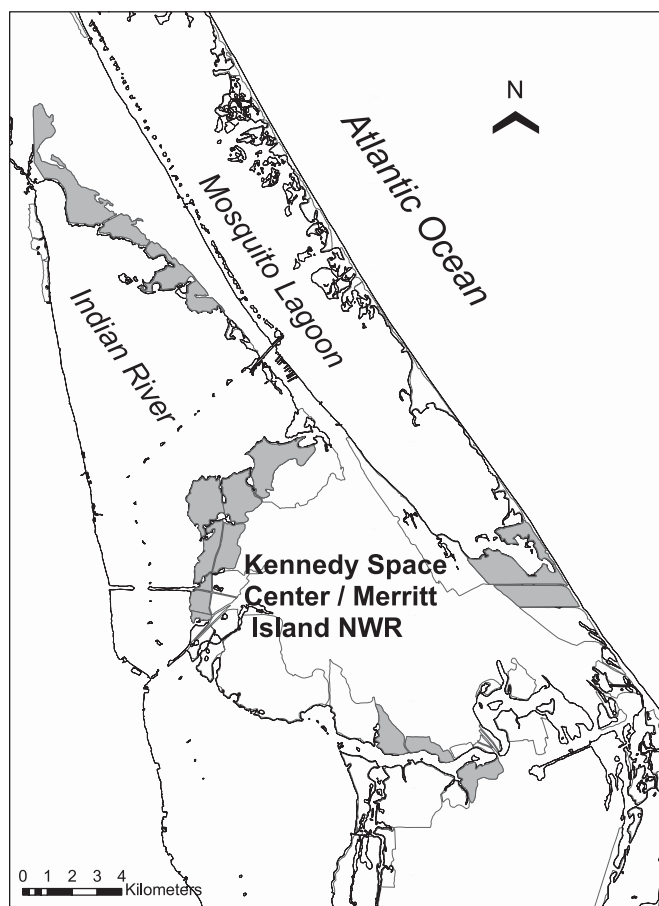
FIGURE 1.   Map of study site showing location of impoundments studied at the Kennedy Space Center/Merritt Island National Wildlife Refuge.

area is isolated from the nearest ocean inlet and the range of the tides in it is very low (<1 cm; Smith 1987). In this region, seasonal and wind-driven water level fluctuations are of much greater importance (Smith 1993). The habitat within impoundments is predominantly a heterogeneous mixture of open water and vegetated cover types, with tall marsh grass (e.g., *Spartina bakeri*) and short marsh vegetation (e.g., *Distichlis spicata*, *Batis maritima*) predominating in vegetated areas (Schmalzer 1995). We chose 18 impoundments in three areas of KSC/MINWR for observations of foraging wading birds (Fig. 1). During the first year of observation this area was experiencing a severe drought, and water levels were unusually low in many impoundments by midsummer. Rainfall and water levels during the second year were more typical.

OBSERVATIONS OF GROUP FORAGING

To determine the effect of group size and prey density on foraging rates between and within species, from January 2002 to June 2003 we observed wading birds' foraging behavior and sampled prey at locations where the birds were foraging. We chose the three most abundant species of piscivorous wading birds at KSC/MINWR (Stolen et al. 2002): the Great Egret, Snowy Egret, and Tricolored Heron. Observations were made between sunrise to 6 hr after sunrise, the period of largest wading bird aggregations and greatest feeding activity in many areas studied (Hom 1983, Cézilly et al. 1990, Kersten et al. 1991). To identify foraging groups for sampling unambiguously, we defined groups as three or more individuals foraging with distances between them of 10 m or less. We chose this distance as the maximum at which it seemed plausible that a wading bird could disturb a fish, and it is similar to that used to define groups in other studies (Erwin 1983a, Wiggins 1991, Master et al. 1993). We defined classes of group size as solitary, small (2–10 individuals), medium (11–50 individuals), and large (>50 individuals). To simplify the study design, we included only birds foraging in sites lacking dense emergent vegetation; this is the most common type of foraging habitat used by aggregations of wading birds at KSC/MINWR (Breininger and Smith 1990, Stolen et al. 2002, Stolen 2006).

During each observation session, we randomly selected a solitary individual or group of foraging birds for sampling as follows. First, we randomly chose a focal impoundment and direction of travel (when possible). Then we selected the first individual or group encountered in the impoundment that was of the target size and habitat class (sites lacking dense emergent vegetation). Within groups, we selected individuals by pointing the spotting scope at the group and choosing the first individual that moved within the field of view. We chose wading birds for observation to equalize sample sizes among group-size categories and took care that the distance of potential observation units from the impoundment's perimeter dike did not influence the choice of sampling unit. Some of the subjects made no strikes (successful or unsuccessful) during the entire time observed. During subsequent analysis, we chose to exclude these individuals, considering them to not be engaged in active foraging during the time observed. These individuals were most likely resting between bouts of foraging (Bildstein 1983), and their inclusion in statistical analysis may have biased the results. Although differences in such resting behavior may have important implications for the economics of foraging behavior, they were not the focus of our study and including them would have greatly complicated the statistical analysis.

Wading birds were observed from a distance of 100–350 m through a 15–60× spotting scope. We measured the foraging behavior of each individual observed for 1 to 3 min, recording its total number of strikes, number of successful captures, and number of steps taken. We attempted to observe each bird for 3 min, but sometimes a bird left the site or became obscured, thus ending the observation period; only observations of at least 30 sec were included in the data. When observations were made within groups, we observed the second or third individuals of a species for 1 min only. This was done to reduce the time between the observations of foraging and the measurement of the prey density at the site.

When possible, we recorded the length (estimated in comparison to bill length) and identity (fish versus nonfish) of prey items ingested (Bayer 1985). Other variables recorded for each individual observed were presence or absence of emergent or submerged vegetation, group size and species composition, water depth (estimated in comparison to leg length), distance to nearest other wading bird at start of observation, nearest distance to other wading bird during observation, sizes of prey captured (estimated by bill length), any aggressive behavior towards or from another forager, movements other than walking, distance to perimeter dike, distance to observer, and location.

For use in analyses, we calculated capture rate from behavioral data. The number of captures min^{-1} was based on the number of prey items captured; this could be detected because wading birds usually make a distinctive head-jerking motion when swallowing prey items. We calculated the mean length of prey items for all individuals for which data were available, converting lengths estimated from the proportion of bill lengths to millimeters on the basis of mean measurements of bills of museum specimens (E. Stolen, unpubl. data).

Immediately after foraging observations, we estimated prey abundance by making three tosses of a 1-m^2 throw trap (Kushlan 1981). This type of sampling gear has been shown to produce accurate estimates of nekton abundance (Chick et al. 1992, Jordan et al. 1997). During prey sampling, researchers first approached the sample site by walking slowly, then tossed a 1-m^2 throw trap from a distance of 1–2 m. Once the trap landed, researchers quickly secured the edges of the trap against the substrate. Fish were then scooped from the trap with a 40- by 30-cm dip net with 2-mm mesh. If vegetation within the trap impeded movement of the dip net it was removed. When the large dip net was scooped three times without catching a fish, we used a 15- by 10-cm dip net with 2-mm mesh, which was more effective in scraping along the edges and into the corners of the trap. The sample was completed when the smaller dip net was scooped three times without catching a fish. We measured the first 30 individuals of each species captured in each throw-trap deployment to the nearest millimeter and estimated the mass of these fish with species-specific regression equations developed for fish captured in other impoundments at KSC/MINWR (Stevens 2002). For each deployment of the throw trap we also recorded water depth, water temperature, salinity, presence of submerged aquatic or emergent vegetation, GPS coordinates, and the overall vegetation of the foraging site. Following sampling at the foraging site, we also took prey samples at a paired random location within the same habitat type 100–200 m from the foraging site. We chose paired random locations by first randomly selecting a compass bearing, then sampling the nearest area of similar habitat at a distance randomly chosen between 100 and 200 m from the point of foraging observations. If this procedure resulted in a site outside the impoundment, we chose a new random bearing. Paired random sites were sampled by the same procedures as foraging sites.

For each sample site (used and paired-unused) we calculated the fish density, estimated prey biomass, and also the mean length and mean biomass per individual fish. Within a sample, we estimated wet prey biomass by multiplying the mean biomass of each species within the sample by the number of individuals of that species. We also included the biomass of shrimp (*Palaemonetes* sp.) in samples, using 0.0817 g as the mean mass of a shrimp (Gilmore 1998).

STATISTICAL ANALYSIS

Foraging-rate models. The response variable from our observational design (captures per minute) was a count adjusted for effort, which is best modeled with a generalized linear model with a log link and Poisson error assumed for residuals (Zuur et al. 2009). We included sample site as a random effect in all models to account for the correlation between individuals sampled within a group. This allowed the correct number of degrees of freedom to be used in estimating effect sizes and also accounted for the correlation between individuals sampled within groups due to environmental variables not measured (Zuur et al., 2009). The statistical models were specified as generalized linear mixed models (log link, Poisson error) of the number of captures for each bird, with an offset for the length of observation per individual (included in models as the natural log of minutes observed). Models were fit in R version 2.12.1 (R Development Core Team 2010) by the package lme4 (Bates and Maechler 2010). Their fit was checked by visual diagnostic plots of residuals. We calculated predicted confidence intervals for graphs in R by following supplementary materials for Bolker et al. (2009). To help quantify the predictive power of models we calculated the Nagelkerkle R^2 of a given model (M_1) as [1 – exp(–2/sample size × log likelihood M_1 – log likelihood null model)]/[1 – exp(–2/ sample size × log likelihood null model)] (Nagelkerkle 1991, Anderson 2008) and the explained deviance as (null deviance – residual deviance)/null deviance (Zuur et al. 2009). Effect sizes are reported as the model's parameter estimate and the associated SE.

Because the data resulted from a planned observational study there was a design-based model relating the response variable (capture rate) and the explanatory variables measured (group size category and species), represented as capture rate ~ group size × species. This model included the effect of an interaction between group size and species, which allowed a different effect of group size on capture rate for each species. We also investigated reduced models based on the design model that dropped some of the terms (i.e., the interaction term and group size and species main effects). In addition, because we could not manipulate field sites, we also recorded several auxiliary environmental variables at each site (prey density, prey biomass, water depth, and type of vegetation) and considered additional hypotheses that included these factors. Thus we formulated an a priori set of hypotheses offering alternative explanations of how these variables influenced the capture rate of foraging wading birds and evaluated the relative support for each model by the relative Kullback–Leibler information distance of that model, measured by

the adjusted Akaike information criterion or AIC_c (Burnham and Anderson 2002). Each alternative hypothesis was translated as a model relating the response variable (captures min^{-1}) with a set of predictor variables. Following model selection, we investigated post hoc whether a two-category group-size variable that collapsed the three group-size categories (i.e., solitary versus group) had more support than the originally measured four-category group-size variable by including either group-size categorical variable in the best-supported models.

We also investigated step rate (paces min^{-1}) by an approach similar to that used for the capture models. The statistical models were specified as generalized linear mixed models (log link, Poisson error) of the number of paces made by each bird, with an offset for the length of observation per individual and sample site as a random effect. Models were fit and evaluated and predictions of the best model were graphed by the statistical procedures described above for capture models. Because collecting the data on stepping was not the main purpose of the observational study, we investigated only a reduced set of models: a model with an interaction between group size (four levels) and species and all simpler models with terms removed sequentially, and a model with the two-level group size (solitary versus group) and species interaction and all simpler models with terms dropped sequentially.

Fish abundance and size. We measured prey density (number of individuals m^{-2}), biomass (total mass of individuals m^{-2}), and prey size (mean length and mass of individual items) at sites used by wading birds and at paired random sites. The data were aggregated for the three prey samples at each site. To quantify differences in the abundance and size of fish between sites, we calculated the mean and 95% confidence intervals and used paired *t*-tests for used vs. random sites and unpaired *t*-tests for sites used by groups vs. solitary individuals. Because the distributions of density and biomass were skewed, we transformed data to better meet the assumptions of the test as ln(density or biomass +1); we back-transformed estimated values reported as exp(estimate) − 1. The directions of the alternative hypotheses were that density and biomass were greater at used sites and at sites with groups (one-tailed tests). To quantify differences in the mean length and mean mass of individual fish at used and paired random sites, we calculated the mean and 95% confidence intervals and used paired *t*-tests. The directions of the alternative hypotheses were that mean length and mass of individual fish were greater at used than at paired random sites (one-tailed tests).

We also investigated how the size of prey captured during the foraging observations differed by wading bird species and group size. We used only one observation for each species within each group, thus avoiding complications due to multiple observations within groups. Because sample sizes were small, we investigated only a few simple linear regression models relating length of captured prey and the species and group effects (a model with the species × group interaction, a model with the additive effects of species and group, and a model with each main effect alone). We used the criteria for model selection

described above. For all statistical calculations we used R version 2.12.1 (R Development Core Team 2010).

RESULTS

FORAGING RATE OF HERONS

Between January and May 2001 and March and May 2002, we recorded the foraging behavior of 137 wading birds foraging in aggregations ranging in size from 1 to 450 individuals at 62 sites; 15 individuals that made no strikes (successful and unsuccessful capture attempts) during the observation period were excluded from the analysis. The best-supported model had an interaction between species and group size (i.e., a different group-size effect for each species) with an Akaike weight of 0.33 (Table 1). This model had a Nagelkerkle $R^2 = 0.31$ and an explained deviance of 0.85. Diagnostic plots of residuals showed no serious lack of fit, although there were several large negative residuals due to a few birds that made no captures during the time they were observed. This model predicted that Snowy Egrets foraging alone captured prey at a rate higher than they did in any size group (Table 2, Fig. 2). In contrast, the model predicted that Great Egrets foraging in groups did better than solitary individuals, and the effect of group size appeared to taper as group size increased (Fig. 2). For the Tricolored Heron the model predicted a pattern similar to the Great Egret, but the effect of group size was estimated with less precision (i.e., large standard errors and resulting 95% confidence intervals). When group size was treated as a binary variable (groups versus solitary individuals) in the post hoc analysis, this model was preferred with an evidence ratio of 6.8 (i.e., on the

TABLE 1. The best-supported models describing alternative hypotheses relating herons' rate of capture success with species, group size, and environmental covariates. The models are ranked in order of decreasing support. Of the 28 models considered, only those with a combined Akaike weight of 0.92 are shown.

Model[a]	K	ΔAIC_c [b]	w_i
group × sp	13	0.00	0.33
group × sp + mass	14	2.43	0.10
group × sp + depth	14	2.54	0.09
group × sp + prey	14	2.55	0.09
group × sp + fish	14	2.56	0.09
group × sp + veg	14	2.60	0.09
group × sp + mass + depth	15	4.92	0.03
group × sp + mass + veg	15	5.08	0.03
group × sp + fish + depth	15	5.14	0.03
group × sp + prey + depth	15	5.15	0.02
group × sp + prey + veg	15	5.19	0.02

[a]All models included a random effect for the foraging group of the observations. Multiplication signs indicate interactions; the main effects are not listed but were always included in such models. Covariates: group = group size category, sp = species of heron, mass = mass of prey, depth = depth of water at sample site, prey = density of prey, fish = density of fish prey only, veg = vegetation category of sample site.
[b]The best-supported model had $AIC_c = 223.88$.

TABLE 2.   Fitted parameter estimates for generalized linear mixed models of herons' capture rate (fish captured min^{-1}) as a function of group size and species. Captures ~ grpCat × species + (1 | sample) was the best supported of the a priori model set and had the interaction between group size (four levels) and species (three levels). Captures ~ Group.bin × species + (1 | sample) substituted a two-level group-size variable (solitary versus group) in place of the four-level group variable and had more support than the a priori best model.

Parameter	Estimate	SE	z	$P(>|z|)$
Captures ~ grpCat × species + (1 | sample)				
Intercept	−0.80	0.38	−2.08	0.04
grpCat = small	0.51	0.47	1.08	0.28
grpCat = medium	0.89	0.54	1.65	0.10
grpCat = large	0.21	0.48	0.45	0.66
Species = Great Egret	−0.47	0.62	−0.76	0.45
Species = Snowy Egret	1.32	0.55	2.39	0.02
grpCat = small; species = Great Egret	0.05	0.72	0.07	0.94
grpCat = medium; species = Great Egret	0.71	0.77	0.92	0.36
grpCat = large; species = Great Egret	1.12	0.67	1.66	0.10
grpCat = small; species = Snowy Egret	−1.44	0.70	−2.04	0.04
grpCat = medium; species = Snowy Egret	−1.80	0.76	−2.37	0.02
grpCat = large; species = Snowy Egret	−1.92	0.66	−2.92	0.00
Variance due to random effect of sample	0.44			
Captures ~ group.bin × species + (1 | sample)				
(Intercept)	−0.81	0.39	−2.07	0.04
Group.bin = group	0.57	0.43	1.33	0.18
Species = Great Egret	−0.47	0.63	−0.75	0.45
Species = Snowy Egret	1.32	0.56	2.34	0.02
Group.bin = group; species = Great Egret	0.79	0.66	1.20	0.23
Group.bin = group; species = Snowy Egret	−1.85	0.61	−3.03	0.00
Variance due to random effect of sample	0.47			

basis of data it was nearly seven times more likely to be the best model among the models considered). Residual diagnostic plots showed no serious lack of fit, and this model had a Nagelkerkle R^2 = 0.22 and an explained deviance of 0.89. The two-category and four-category group-size models showed a similar effect of group size by species (Table 2, Fig. 3).

None of the models that contained the auxiliary variables measured at the sample locations (prey density, prey biomass, water depth, and presence of vegetation) had greater than 10% of the combined Akaike weight for the set of a priori models (Table 1). Although several of these models, which added various environmental factors to the species-by-group-size interaction, appeared to have some support on the basis of information-theoretic model selection, these variables did not improve a model's fit as measured by its log-likelihood (Table 1). Furthermore, examination of model parameters showed that the parameter estimates for these extra terms had low precision, affirming the strength of support for the highest-ranked model and its inferential value in this study.

The best-supported model of stepping rate had an interaction between species and group size (i.e., a different group-size effect for each species) with an Akaike weight of nearly 1.0 (this model had virtually all the support among the models considered). This model had Nagelkerkle R^2 = 0.95, explained deviance of 0.75, and the diagnostic plots of residuals showed
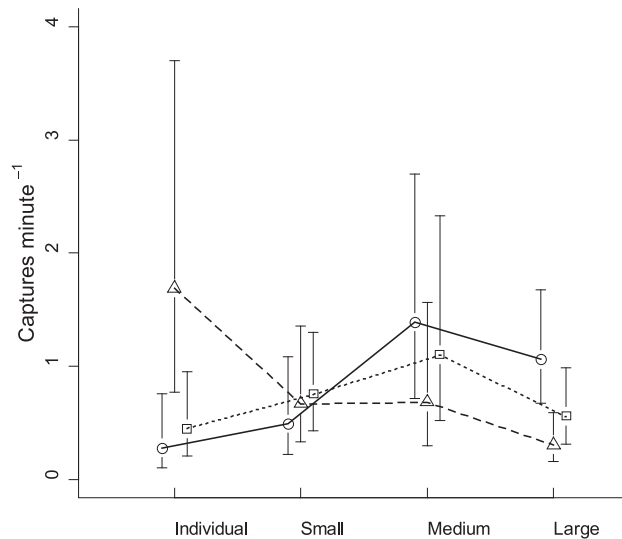

FIGURE 2.   Estimated rate of prey capture by herons foraging alone and in groups of three size categories, based on the best-supported model from this study. Circles, Great Egret; triangles, Snowy Egret; squares, Tricolored Heron. The Great Egret's capture rate increased in medium and large groups; the Snowy Egret's capture rate was lower when the birds were in groups than when foraging alone. Error bars are 95% confidence intervals including the variation due to the random effect of site. Group-size classes are solitary, small (2–10 individuals), medium (11–50), and large (>50).
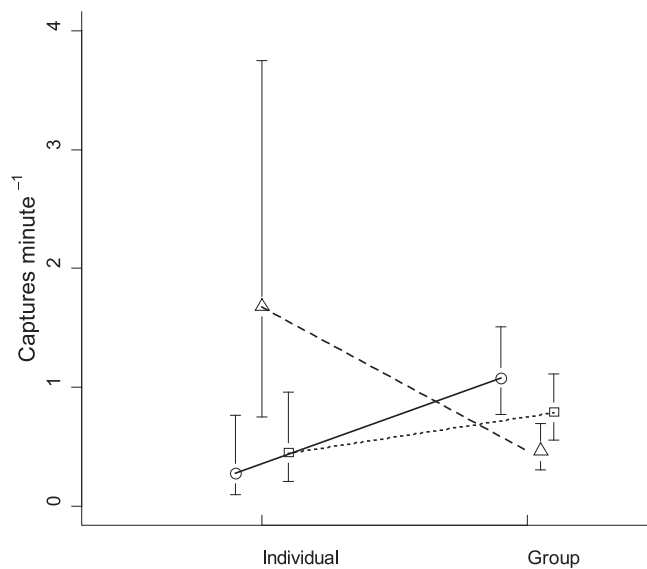
FIGURE 3.   Estimated rate of prey capture by herons foraging alone and in groups of any size, based on the best-supported post hoc model from this study,. in which a binary variable was substituted for the four-category group-size variable in the best a priori model. Circles, Great Egret; triangles, Snowy Egret; squares, Tricolored Heron. Great Egrets showed an increase in capture rate when foraging in groups, while Snowy Egrets had a lower capture rate in groups than when foraging alone. Error bars are 95% confidence intervals including the variation due to the random effect of site. Group-size classes are solitary, small (2–10 individuals), medium (11–50), and large (>50).
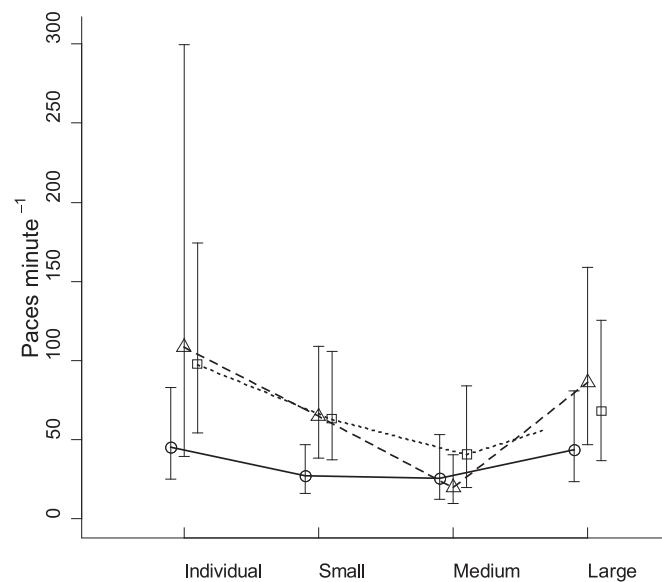

FIGURE 4.   Estimated stepping rate of herons foraging alone and in groups of three size categories, based on the best-supported model. Circles, Great Egret; triangles, Snowy Egret; squares, Tricolored Heron. All species showed a trend of reduced stepping rate in small and medium-sized groups. Error bars are 95% confidence intervals including the variation due to the random effect of site. Group-size classes were solitary, small (2–10 individuals), medium (11–50), and large (>50).

no serious lack of fit. This model predicted that all three species showed a U-shaped response of stepping rate to group size, but the group-size effect was poorly estimated (Fig. 4).

FISH DENSITY AND BIOMASS AND SIZE OF PREY CAPTURED

Both the density and biomass of fish were greater at sites used by wading birds than at the paired random sites, although the difference was not significant for density (Table 3). Both the density and biomass of fish was greater at sites used by groups of wading birds than at sites used by solitary individuals, and both differences were significant (Table 4). Both mean length and mean biomass of individual fish were greater at used than at unused sites (Table 3). The mean length and mean biomass of individual fish at sites used by groups of wading birds and at sites used by solitary individuals did not differ (Table 4).

The best-supported model of captured prey size included only an effect for species (Table 5). This model indicated that Snowy Egrets captured smaller prey than did either Tricolored Herons or Great Egrets (Table 6, Fig. 5). The models with the group category (solitary versus group) had less support, and the group-category effect was poorly estimated (i.e., there was no evidence for a difference in size of prey captured by birds foraging alone or in groups).

DISCUSSION

Consistent with the social-facilitation hypothesis, Great Egrets had higher capture rates when foraging in groups than solitarily, and the effect tapered off as group size increased. Tricolored Herons showed a similar pattern, although estimates of the effect sizes were less precise. Because we measured and controlled for prey density and environmental factors related to prey availability, the observed benefit of foraging in groups

TABLE 3.   Comparison of fish density and biomass and the mean length and mass of individual fish at sites used by wading birds and the paired random sites. The numbers within parentheses are 95% confidence intervals of the estimates.

	Used		Random		t	df	P
Density (fish m^{-2})	6.85	(4.77, 9.79)	5.29	(3.48, 7.95)	1.47	61	0.07
Biomass (g m^{-2})	3.61	(2.47, 5.21)	2.30	(1.51, 3.44)	2.36	61	0.01
Mean length (mm)	23.56	(21.98, 25.13)	22.14	(20.64, 23.64)	1.83	54	0.04
Mean mass (g)	0.73	(0.43, 1.03)	0.47	(0.37, 0.57)	2.15	54	0.02

TABLE 4. Comparison of fish density and biomass and the mean length and mass of individual fish at sites used by solitary wading birds and sites used by groups.

	Individual		Group		t	df	P
Density (fish m^{-2})	4.28	(1.87, 9.33)	8.54	(5.79, 12.52)	1.82	60	0.04
Biomass (g m^{-2})	2.31	(1.00, 4.89)	4.43	(2.88, 6.72)	1.64	60	0.05
Mean length (mm)	24.22	(21.71, 26.73)	23.18	(21.27, 25.09)	0.65	57	0.74
Mean mass (g)	0.62	(0.33, 0.9)	0.77	(0.37, 1.17)	0.50	57	0.31

for these species was not confounded with differences in prey availability. This finding was consistent with the results of Gawlik (2002), who characterized the Great Egret's foraging strategy as that of an "exploiter," meaning that it remains at sites as prey density declines rather than searching for new sites. Several previous studies have also found that Great Egrets and Tricolored Herons exploit a range of habitat conditions wider than do other species, including the Snowy Egret (Powell 1987, Smith 1995, Gawlik 2002). Adaptations allowing individuals to take advantage of enhanced foraging success in groups would benefit individuals of those species that tend to remain at sites until they are depleted rather than search for new sites.

Contrary to the prediction of a social-facilitation effect, Snowy Egrets foraging in groups captured prey at a rate lower than did solitary foragers. However, this difference in foraging behavior may make sense in light of recent studies of foraging and searching behavior of herons. For example, Gawlik (2002) characterized the Snowy Egret as a "searcher" in foraging strategy, meaning that it specializes in finding and exploiting patches of high quality but abandon patches as their quality declines due to exploitation. Our results provide another mechanism by which patch quality declines for searchers remaining within patches; as additional foragers arrive at a site an individual's foraging-success rate declines because of interference. If Snowy Egrets require high-quality prey patches, it may make sense for them to exploit such sites quickly after locating them and then move on to new sites as prey becomes depleted or patch quality declines. If they

TABLE 5. Linear models of mean size of prey captured by herons. Models describe alternative hypotheses relating mean size of prey captured with group membership status and species.

Model[a]	K	ΔAIC_c[b]	w_i
Prey size ~ species	4	0.00	0.63
Prey size ~ species + group	5	1.85	0.25
Prey size ~ 1	2	4.57	0.06
Prey size ~ species × group	7	6.00	0.03
Prey size ~ group	3	6.31	0.03

[a]Multiplication sign indicates interaction; the main effects are not listed but were always included in such models. Null model (sample only) indicates a model with only terms for the intercept and the random effect of foraging group. Covariates: group = group versus solitary, species = species of heron.
[b]The best-supported model had $AIC_c = 405.05$.

TABLE 6. Fitted parameter estimates for best linear model of mean size of prey captured by herons as a function of group and species.

Parameter	Estimate	SE	t	$P(>|t|)$
Intercept	23.99	1.96	12.22	0.00
Snowy Egret	−8.47	2.78	−3.05	0.00
Tricolored Heron	−3.67	2.59	−1.42	0.16

employ this strategy, then they may not be adapted to conditions of group foraging and may thus be unable to exploit strategies benefiting individuals foraging in groups.

Several studies have described the Snowy Egret as a core species around which social foraging groups form (Caldwell 1980, 1981, Master 1992, Smith 1995). This fact seems to make puzzling our finding that Snowy Egrets had lower foraging success in groups than when foraging alone. One possible explanation is that Snowy Egrets may prefer sites with higher prey density and thus tolerate the presence of other foragers. Offsetting the costs of group foraging by choosing sites with higher prey density, however, does not resolve why Snowy Egrets have conspicuous white plumage, which has been shown to attract
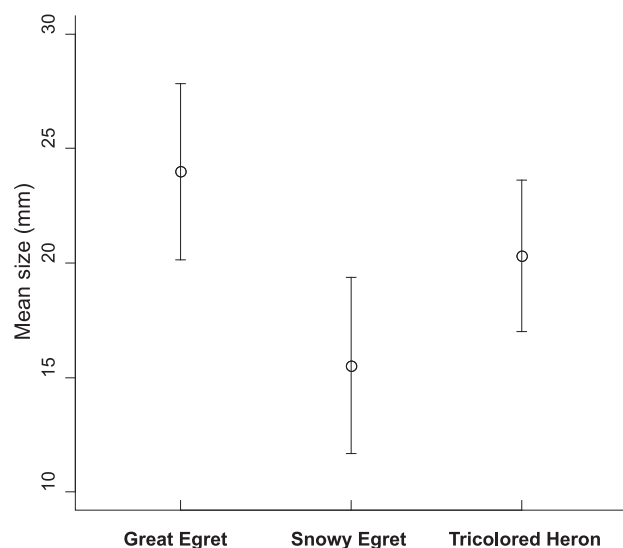

FIGURE 5. Mean length of fish captured by wading birds estimated by the best-supported model based on data from foraging observations. Error bars are 95% confidence intervals of the predictions.

other foragers (Cadwell 1981, Master 1992). One answer may be that under circumstances different from those we studied, individual Snowy Egrets may derive benefits from the presence of other foragers. One possibility was raised by Caldwell (1981), who speculated that Snowy Egrets benefited from proximity to subordinate species (e.g., Tricolored Heron, Little Blue Heron) that they could displace from prey. In our study area, the high proportion of dominant Great Egrets in foraging groups (Stolen 2006) may have diminished this benefit. Another possibility is that information about foraging sites is more important to individuals than is maximizing short-term foraging success (Valone 1991). In support of this explanation is the fact that more than half of the Snowy Egrets followed from colonies in KSC/MINWR in a related study (Stolen et al, 2007) left in groups and almost all joined foraging groups.

Decreasing energy expenditure might be another benefit to individuals choosing to forage in groups. Some studies have found that wading birds can benefit by saving energy while foraging in groups over energy expended by those foraging alone (Hafner et al. 1982, Master et al. 1993). In our study, for all species, the stepping rate of birds foraging in small and medium groups was lower than that of individuals or birds foraging in large groups, a trend that was strongest for the Snowy Egret and least pronounced for the Great Egret. This potential benefit of group foraging might explain why Snowy Egrets choose to forage in groups despite a capture rate reduced below that of those foraging alone.

Wading birds foraged at sites with prey quality (abundance and size of individual fish) higher than at unused sites, and foraging groups occurred at sites with higher prey quality than did solitary individuals. This finding is similar to others that have shown that when foraging wading birds can find and exploit higher-quality sites (Hafner and Britton 1983, Draulans 1987, Master et al. 2005). The lack of strong evidence for a positive relationship between prey density and capture rate for any species we studied was unexpected since many have suggested that wading bird populations require prey to become concentrated in order for individuals to forage efficiently in groups (Kushlan 1976b, Hafner et al. 1982, Cézilly et al. 1990, Gawlik 2002, Miranda and Collazo 1997, Collazo et al. 2010). A plausible explanation for this seeming discrepancy is that the ranges of prey density we recorded, while not markedly high, were still within the range of maximum foraging efficiency (Krebs 1974, Miranda and Collazo 1997). If true, this suggests that at least under some circumstances, prey density is not the most important factor affecting wading birds' foraging success.

An alternative interpretation of our evidence for social facilitation is that we were not able to detect subtle differences in prey density between sites, and these differences explain the patterns in capture rate by species and group sizes. Although throw-trap sampling has been shown to be capable of producing unbiased estimates of density, species composition, and size distribution (Jordan et al. 1997, Able 2005), our method of sampling fish may have missed schools of fish. In the marshes we studied fish are patchily distributed at several scales (Stolen 2009), causing high variability in our samples and thus lowering power to detect differences in prey density between sites. Despite this caveat, we believe that not finding an effect of prey density on capture rate implies that such an effect was not strong. Another piece of evidence supporting the limits of prey density as an explanation for the differences in capture success for birds in groups of different sizes was that the three species responded differently within the same groups. Thus individuals exposed to similar levels of prey density had different responses, leaving group size as a more plausible explanation.

Our finding that Snowy Egrets captured smaller prey than did either Great Egrets or Tricolored Herons agrees with previous studies (Kent 1986, McCrimmon et al. 2001). It is tempting to speculate that the Snowy Egret's preference for smaller prey is somehow related to the difference between the species in the effect of group size on capture rate. Herons often prefer larger fish (Britton and Moser 1982, Trexler et al. 1994), and selecting larger fish has energetic value (Maccarone and Brzorad 2007), although fish that are too large are avoided (Werner et al. 2001). If smaller fish had a different behavioral response to disturbance by the presence of foraging wading birds, this might explain the differences in capture rate between the Snowy Egret and the other species. Although estimating prey size from bill length is feasible (Cézilly and Wallace 1988, Butler 1990), errors in this estimation could have influenced our results (Bayer 1985). For example, if for some reason we tended to underestimate prey size by comparison with the Snowy Egret's bill, this might have caused the observed pattern of Snowy Egrets capturing smaller prey. However, since of the three species studied the Snowy Egret has the smallest bill, this does not seem a likely explanation.

Our results underscore the fact that wading birds are highly opportunistic foragers capable of rapid responses to changing habitat conditions, and that the benefits and costs of feeding in aggregations depend on the context within which they occur (e.g., prey type and density, vegetative cover, water depth, turbidity, composition of aggregations; Strong et al. 1997, Gawlik 2002, Frederick and Ogden 2003). Managers might use this information to manipulate habitat to benefit wading birds species that depend on group foraging. For example, to enhance opportunities for social facilitation by group foragers, managers could manipulate hydrology and vegetation structure to enhance conditions in which cryptic prey can be encountered and disturbed by foraging groups. Optimal foraging conditions have been shown to be important during periods of high energetic demands such as nesting or migration (Frederick and Spalding 1994).

ACKNOWLEDGMENTS

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