Sociality Among Foraging Ardeidae: Does Plumage Coloration Influence Nearest-Neighbor Spacing?

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ABSTRACT.—Increased sociality in herons, family Ardeidae, is often considered to be associated with the occurrence of white plumage. If white plumage increases sociality, we hypothesized that white-plumaged birds should forage closer to one another and dark birds should remain more solitary. We tested this hypothesis by investigating the inter-individual spacing (nearest neighbor distance) in two pairs of closely related species that differ in plumage coloration: (1) Great Blue Heron (*Ardea herodias*)/Great Egret (*A. alba*) and (2) Little Blue Heron (*Egretta caerulea*)/Snowy Egret (*E. thula*). All birds observed were in adult plumage. We recorded distances to nearest conspecific, nearest congeneric, nearest white (regardless of species) and nearest dark bird to each focal bird within a given (focal) pond. Because species occurred in varying numbers, we compared the observed mean distances with randomly generated distances based on the total number of birds in the pond. All observations were conducted under steady water levels, avoiding drying ponds as this might concentrate prey. We found that Snowy Egrets were significantly farther from conspecifics and dark congenerics (Little Blue Herons) than expected under a null model of random spacing within the focal pond. Little Blue Herons also were spaced farther apart from white congenerics (Snowy Egrets) than expected. Great Blue Herons and Great Egrets exhibited no distinct social tendencies and neither avoided nor preferred foraging near other herons. Our results do not support the hypothesis that white-plumaged birds exhibit increased social tendencies relative to dark-plumaged birds within a given pond.

INTRODUCTION

Current phylogenies of the Ardeidae reveal closely related species that differ considerably in plumage coloration, with one species being all-white and the other darkly colored (*e.g.,* Snowy Egret and adult Little Blue Heron; Sibley and Ahlquist, 1990; Sheldon, *et al.*, 1995; Sheldon and Slikas, 1997). Biologists have long been intrigued by dichromatisms and the apparent repeated independent evolution of white plumage in herons. White plumage has been suggested to facilitate sociality in herons for either enhanced foraging efficiency, protection from predators, or reduced search time (Kushlan, 1976, 1977; Erwin, 1983; Caldwell, 1986; Beauchamp and Heeb, 2001; Gawlik, 2002).

Members of the order Ciconiiformes often form large mixed-species aggregations (flocks) both when foraging and nesting. Herons may form foraging aggregations for increased foraging success (Russell, 1978; Caldwell, 1981; Erwin, 1983; Cezilly *et al.*, 1990) or reduced energy expenditure (Kushlan, 1978a, b; Master *et al.*, 1993). Increased foraging success or "positive interference" (*see* Mock, 1980) refers to the situation where an individual's

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foraging efficiency is significantly enhanced by the presence of another forager. Snowy Egrets (Master *et al.*, 1993) and Great Egrets (Wiggins, 1991), two white-plumaged species, have higher capture rates and efficiencies when foraging in flocks. However, it is difficult to differentiate between the neighbor's presence and the concentration of food resources as the key contributor to increased foraging efficiency (Krebs and Davies, 1978; Mock, 1980). Social aggregations may also be a product of many birds using the same (best) foraging sites where prey are concentrated and available (Cezilly *et al.*, 1990; Master *et al.*, 1993).

Herons may also utilize social aggregations for protection from predators. These flocks may be maintained in order to enhance predator detection through shared vigilance ("many eyes" hypothesis, Pulliam, 1973) or by dilution or confusion effect ("selfish herd" hypothesis, Hamilton, 1971). White Ibis (*Eudocimus albus*) spend less time being "vigilant" while foraging in the center of large flocks than individuals foraging at the periphery of the large flocks or in small flocks (Petit and Bildstein, 1986).

Predation has been suggested to be a major selective force in the maintenance of color dimorphism in various taxa (Jones *et al.*, 1977; Endler, 1978), as well as in herons (Caldwell, 1986). Assuming no sensory bias, white-plumaged birds are generally more visible to avian predators while dark morphs tend to be more cryptic (Caldwell, 1986). Because white birds are less cryptic, it is perhaps more beneficial for white birds than dark birds to forage in a flock to minimize predation risk (Master, 1992). This would represent a trade-off between minimizing predation and minimizing resource competition. Dark birds, with lower predation risk, should forage alone to reduce competition. Often in flocks, white birds foraged more often in the center and darker birds foraged along the perimeter (Caldwell, 1986; Master, 1992). Caldwell (1986) reported that hawks were more attracted to white decoys than to dark decoys. Caldwell (1986) also found solitary herons more likely to be preyed upon than individuals in flocks. Holyoak (1973) sampled the occurrence of the plumage dimorphic Eastern Reef Herons in the Polynesian Islands and attributed distributional differences to birds attempting to match their substrate for avoiding aerial predators. Thus, the influence of predatory pressures should be considered when investigating the causes and/or consequences of plumage polymorphism.

We have been investigating the ecological significance of white plumage in the Ardeidae as it relates to flock formation (Green and Leberg, 2005a), crypsis to aquatic prey (Green and Leberg, 2005b) and foraging behavior (Green, 2005). Here we assessed the role of white plumage on social interactions among birds within a flock. If white plumage is more visible to predators, differences in plumage coloration may result in white birds exhibiting smaller spacing (inter-individual distances) between one another than spacing between dark birds. Likewise, if white plumage evolved to facilitate social foraging, we would also expect shorter spacing between white birds than between dark birds. While we cannot assess the relative merits of these two hypotheses, we evaluated their common prediction that white-plumaged species should forage closer to one another (conspecifics) than dark-plumaged species. If either of these hypotheses is true, the distance between a white bird and a conspecific should be smaller than the distance between two dark conspecifics. Additionally, we tested the hypothesis that in mixed-species aggregations, the distance between two white birds (regardless of species type) should be closer than that between two dark birds.

METHODS

Study site.—We evaluated inter-individual spacing between foraging herons at a crayfish-rice aquaculture complex near St. Martinville, Louisiana, U.S.A ($30°10'12''$N, $91°44'24''$W). The aquaculture complex is located adjacent to the Atchafalaya Basin, a vast forested wetland that contains over 25 wading bird colonies (Michot *et al.*, 2001). The complex is

heavily used during spring and summer months by both breeding and non-breeding wading birds; therefore, the probability of observing the same bird(s) repeatedly was highly unlikely. We conducted all observations from March–July of 2001–2003 when the ponds were flooded for crayfish production and the various species of Ardeidae had returned from their respective wintering grounds. Observations were done between 0800 and 1200 CST. The crayfish ponds that we sampled ranged in size from 70,200 m^2 (approximately 265 m × 265 m) to 380,000 m^2 (approximately 616 m × 616 m). During crayfish season, ponds are periodically drained for conversion to rice farming. Natural or man-induced pond drainings generally concentrate prey and result in large gatherings of waterbirds at the site (Krebs, 1974; Kushlan, 1976; Mock, 1980). Estimated prey concentrations (per cubic meter) under stable water conditions for crayfish, fish and total prey from nearby rice-crawfish farm that uses the same watershed were 4.16 ± 0.94, 32.08 ± 7.14 and 36.42 ± 7.09, respectively (Fleurry, 1996). Common fish species sampled in these ponds included mosquitofish (*Gambusia affinis*), least killifish (*Heterandria formosa*), sailfin molly (*Poecilia latipinna*) and banded pygmy sunfish (*Elassoma zonatum*). We wanted to investigate inter-individual distances among foraging herons under stable, unchanging water conditions and therefore conducted all observations at ponds where water levels were stable and pond drainings were not occurring.

Study species and observation protocol.—We conducted paired observations on two species' pairs that are closely related and differ considerably in plumage coloration: (1) Great Blue Heron/Great Egret and (2) Little Blue Heron/Snowy Egret. Only adult Little Blue Herons in adult dark plumage were used in the observations. Observations were paired to minimize the effects of external variables (*e.g.,* sunlight, wind, temperature) on our results. The same pond was used for both focal bird observations within the pair to control for variation in habitat among ponds.

Because of the ephemeral composition of wading bird social aggregations, one focal bird from each species was randomly selected for nearest-neighbor observations. Focal birds were randomly selected on each pond by dividing the area into halves; each half chosen was determined by the flip of a coin. Each "half" was subdivided until only one bird of that species remained in the selected "half". A focal bird was only selected when both species of the pair were present in the observation pond. Upon selection of the focal bird, distance (in meters) to the nearest conspecific, nearest alternate plumage color (congeneric) and nearest dark and white birds (non-conspecific or congeneric) was recorded. For example, if a Snowy Egret was the focal bird, we recorded distance to nearest Snowy Egret, distance to nearest Little Blue Heron, and distance to nearest white- plumaged bird and nearest dark-plumaged bird regardless of species. Other white- plumaged birds using the area included White Ibis and Cattle Egret (*Bubulcus ibis*), while other dark plumaged birds included *Plegadis* Ibis and Tricolored Heron (*Egretta tricolor*). Distances between birds were estimated through triangulation using an engineering transit. The total number of conspecifics, congenerics, other white birds and other dark birds in the pond was also recorded. We then repeated this process for a randomly selected focal bird with the alternate plumage color (congeneric). Only one bird per species was selected from each pond for a particular observation period. We conducted our observations at multiple ponds per observation day; thereby, minimizing the probability of the same individuals being used again as focal birds during the same observation day.

Statistical analyses.—For all analyses, we tested the null hypothesis that the distances from focal bird to nearest conspecific, nearest congeneric, nearest white and nearest dark bird were not different between members of each species pair. Because wading bird species often occur in unequal numbers, comparisons of nearest-neighbor distances between species

might be biased. For example, if a pond contains 50 Snowy Egrets and 25 Little Blue Herons, based on random chance alone, one would expect to find the inter-individual spacing between two Snowy Egrets to be lower than the distances between two Little Blue Herons. To correct this bias, we developed a computer routine using SAS (SAS Inst., 1999) that utilizes the number of birds foraging in the same pond as the focal bird to generate a null expectation for the distance to the nearest conspecific and congeneric birds. These null expectations for distance to the nearest member of a species are based on 1000 randomizations of the positions of the birds in the pond. We generated a mean random distance from these 1000 iterations for each paired observation. We conducted a Wilcoxon paired-sample test, due to non-normal distribution of the differences, comparing the observed distances with each mean randomly generated distance to determine if spacing observed between focal bird and closest conspecific/congeneric birds was different than that predicted by random chance (Zar, 1996).

For analysis of inter-individual spacing between focal birds and nearest white/dark birds, regardless of species, we compared distances from focal white and focal dark birds to nearest white bird. We repeated this analysis on the distance from focal white and focal dark bird to the nearest dark bird, regardless of species. Because the number of white birds or dark birds in a pond was constant for both focal species, randomization was unnecessary. We again used a Wilcoxon paired-sample test between each member of the species pair to test the hypothesis that spacing between focal birds and nearest white or nearest dark bird was not different between our two species pairs, great blue herons and great egrets, and little blue herons and snowy egrets. Statistical significance was determined $\alpha = 0.05$ using the critical values of the Wilcoxon T distribution (Zar, 1996). Values reported in the following results are mean differences $\pm$ SE. Values reported in the figures are true mean $\pm$ SE.

<div align="center">RESULTS</div>

Distances to nearest conspecific and nearest congeneric.—We use 11 different crayfish ponds for our nearest-neighbor observations. Mean total number of white and dark-plumaged wading birds present per pond observation was 119.06 ± 0.15; range 8–387 individual birds. Inter-individual distances of Great Blue Heron (GBHE: mean difference $= -9.48 \pm 18.12$, $T_- = 520.0$, $P > 0.50$) and Great Egrets (GREG: mean difference $= 11.42 \pm 10.90$, $T_- = 428.5$, $P > 0.50$) to conspecifics were not different than that of randomly generated distances (Fig. 1). Great Blue Herons (mean difference $= 26.39 \pm 17.24$, $T_- = 356.0$, $P > 0.50$) and Great Egrets (mean difference $= 34.09 \pm 24.74$, $T_- = 370.0$, $P > 0.50$) also did not differ in their inter-individual spacing to congenerics (Fig. 1). Little Blue Herons also did not differ in inter-individual spacing between conspecifics (LBHE: mean difference $= 21.47 \pm 15.99$, $T_- = 205.0$, $P > 0.50$) whereas Snowy Egrets were significantly further away from conspecifics than expected based on random chance (SNEG: mean difference $= 58.85 \pm 21.36$, $T_- = 129.0$, $P < 0.05$, Fig. 2). Snowy Egrets (mean difference $= 44.21 \pm 22.0$, $T_- = 127.5$, $P < 0.05$) were significantly further away from congenerics (LBHE) than expected based on random chance, while Little Blue Herons (mean difference $= 63.03 \pm 26.76$, $T_- = 137.0$, $0.05 < P < 0.10$) tended to be further away from congenerics (SNEG) than expected based on random chance (Figure 2).

Distances to nearest white- and nearest dark-plumaged bird.—Great Blue Herons and Great Egrets did not differ in their distances to the nearest white bird (mean difference $= 5.60 \pm 8.90$, $T_- = 322.5$, $P > 0.10$, Fig. 3) or the nearest dark bird (mean difference $= 15.79 \pm 23.22$, $T_- = 348.0$, $P > 0.50$). Little Blue Herons and Snowy Egrets also did not differ in their distances to nearest white bird (mean difference $= -19.81 \pm 25.42$, $T_- = 238.0$, $P > 0.50$, Fig. 3) or nearest dark bird (mean difference $= 17.81 \pm 25.70$, $T_- = 196.0$, $P > 0.50$).
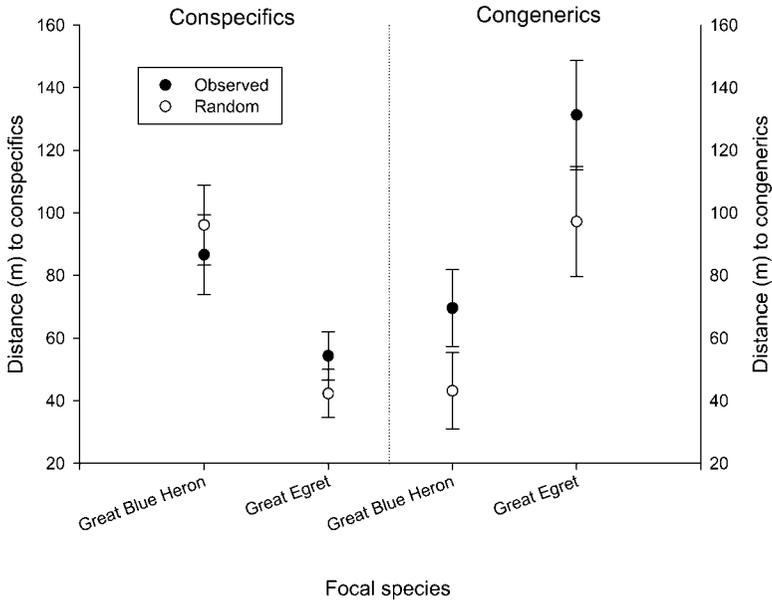
Fig. 1.—Comparison of observed and randomly-generated mean nearest-neighbor distances from focal species to conspecifics and congenerics for Great Blue Herons (N = 39) and Great Egrets (N = 39). Means reported are true means, bars represent 1 SE

DISCUSSION

Distances to nearest conspecific and congeneric.—We examined whether species-specific interactions may be influencing inter-individual spacing among foraging herons. Based on this hypothesis, we predicted that individuals would be closer to conspecifics than distances based on random chance. However, under stable water level conditions, the four species of Ardeidae that we observed did not forage any closer to conspecifics when compared with distances generated under a null model of random spacing. Our research investigated spacing at a fine scale, within an aquaculture pond. Gawlik (2002) demonstrated positive correlations between Snowy Egret densities and other wading birds species at a coarser scale, between ponds. Contrary to our predictions, Snowy Egrets appeared to avoid conspecifics within a given pond. Our results also suggested that Snowy Egrets and Little Blue Herons may actively avoid each other within a given pond. Alternatively, Snowy Egrets may actively avoid Little Blue Herons while Little Blue Herons exhibit no preference/avoidance tendency or vice versa. Great Blue Herons and Great Egrets showed no apparent influence on each other with regard to inter-individual spacing.

Distances to nearest white- and nearest dark-plumaged bird.—Based on the hypothesis that white plumage facilitates sociality, we predicted that white-plumaged birds would forage closer to one another (*e.g.,* conspecifics) than dark-plumaged species. Furthermore, dark-plumaged birds should not differ in their spacing between other dark birds (*e.g.,* conspecifics) or white birds (*e.g.,* congenerics) and that of randomly determined spacing. Contrary to our predictions, we observed that all four species, regardless of plumage coloration, were no closer or farther away from the nearest white or nearest dark birds when compared within each species pair. Our results do not support the hypothesis that white-plumaged herons forage closer to other white birds or that they are more social than dark-plumaged birds.
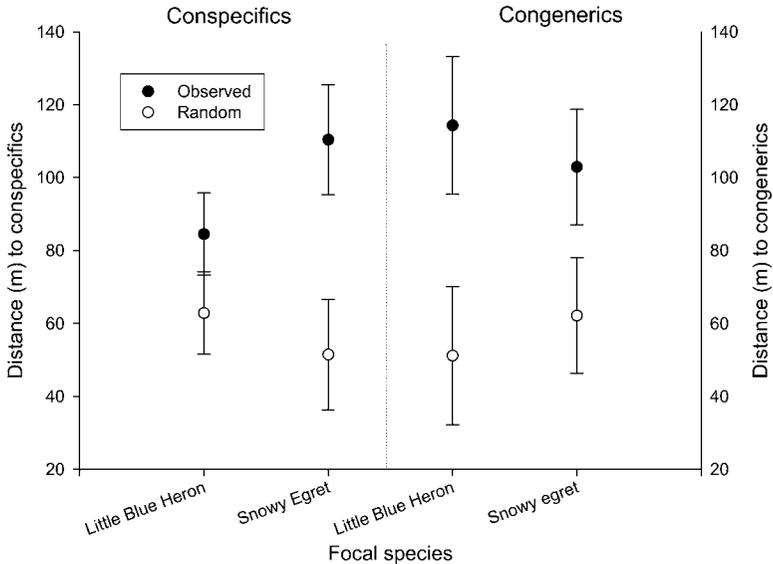
FIG. 2.—Comparison of observed and randomly-generated mean nearest-neighbor distances from focal species to conspecifics and congenerics for Little Blue Herons (N = 28) and Snowy Egrets (N = 28). Means reported are true means, bars represent 1 SE

Our results do not support the hypothesis that white plumage promotes close spatial proximity in foraging herons. Neither white species exhibited any tendencies to aggregate closer to one another than expected based on random chance. Under the hypothesis that white plumage facilitates flocking for protection from predation, dark birds would be expected to forage singly or along the perimeter of a flock. While Little Blue Herons were significantly farther away from Snowy Egrets when compared with random distances, this species showed no discernible "preference or avoidance" to white or dark birds in general. Caldwell (1986) reported increases in nearest-neighbor distances between herons under increased predatory pressures. Intuitively, this appears at odds with the proposed advantages of flocking. Vine (1973), however, suggested that "spacing out" within flocks presents a fragmented target that is difficult for the aerial predator to pinpoint and attack as well as increasing the distance at which a flock can detect a predator.

Many studies of social foraging in wading birds have focused on birds congregated in low-water situations where prey are concentrated or less mobile (Kushlan, 1976; Master, 1992; Maccarone and Parsons, 1994; Bancroft *et al.*, 2002; Gawlik, 2002). Prey that are clumped and restricted in their movement may result in an increase in foraging rates and foraging success for herons (Krebs, 1974; Kushlan, 1976; Gladstone, 1977; Master, 1992). Birds in this enriched resources environment should spend more time foraging and less time protecting a territory. When prey are more dispersed and presumably less restrictive in movement, it may be more profitable for the heron to exert some energy defending a territory. At our study site, we only observed birds during steady water levels, presumably providing a greater chance of prey being dispersed and unrestricted in movement. Thus, our design may have produced different results from studies conducted in low-water environments because of the increased opportunity for birds to be territorial when prey are dispersed. Additionally, we
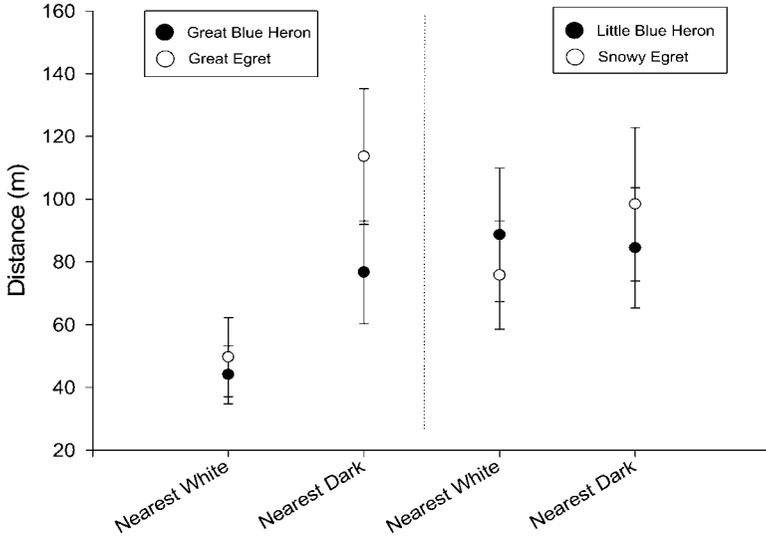
FIG. 3.—Comparison of observed distances from focal white and focal dark species to nearest white and nearest dark bird. We used paired comparisons between Great Blue Herons and Great Egrets (N = 39) and Little Blue Herons and Snowy Egrets (N = 28). Means reported are true means, bars represent 1 SE

only examined inter-individual spacing at a fine scale (within a given pond) and not across adjacent ponds. It is plausible that birds may space themselves out over a greater scale than at what we examined.

Territorial defense of stable and shifting feeding areas is exhibited to some degree by all North American herons (Recher, 1972; Krebs, 1974; Caldwell, 1981; Maccarone and Parsons, 1994; C. Green, pers. obs.). This larger-than-expected spacing between Little Blue Herons and Snowy Egrets was perhaps a result of territorial aggression. Snowy Egrets are known to exhibit territorial aggression under certain environmental conditions and are higher in the interspecific dominance hierarchy than Little Blue Herons (Caldwell, 1979; Maccarone and Parsons, 1994). If territorial aggression is evident from our observations of inter-individual distances with Snowy Egrets, we might expect a similar response from Great Egrets that also exhibit territoriality (Wiggins, 1991). However, our results for Great Egrets showed no preference or avoidance for any particular species or plumage coloration. Low densities of Great Egrets may have diminished our ability to detect increased spacing between birds. Snowy Egrets were the most numerous species on our study site and presumably the large number of birds resulted in more inter-individual interactions.

Payne and Risley (1976) proposed that white plumage may serve as a seasonally operative threat signal. Mock (1980) further elaborated on this hypothesis, suggesting that when prey are dispersed for an extended period of time (e.g., rainy season), herons should defend territories and this defense would consist of two components: threat and aggressive follow-up. Threats need not be active and may simply be a passive signal that requires little energy expenditure, whereas aggressive follow-up requires energy expenditure to chase the interloper out of the area. White plumage may serve as this threat signal by indicating to an intruder that a given area is occupied. Increased conspicuousness of the heron may alert would-be interlopers and presumably allow the territorial occupant longer bouts of foraging

with fewer interruptions. While our research did not directly test this hypothesis, our results show one of the two white-plumaged species foraged farther away from conspecifics, suggesting possible territorial behavior and increased conspicuousness of white plumage.

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