Flock formation and the role of plumage colouration in Ardeidae

M. Clay Green and Paul L. Leberg

Abstract: It has been hypothesized that white plumage facilitates flock formation in Ardeidae. We conducted four experiments using decoys to test factors involved in attracting wading birds to a specific pond. The first three experiments tested the effects of plumage colouration, flock size, and species-specific decoys on flock formation. The fourth experiment examined intraspecific differences in flock choice between the two colour morphs of the reddish egret, *Egretta rufescens* (Gmelin, 1789). Wading birds landed at flocks of decoys more often than single or no decoys ($P < 0.001$) but exhibited no overall attraction to white plumage ($P > 0.05$). White-plumaged species were attracted to white decoys ($P < 0.001$) and dark-plumaged species were attracted to dark decoys ($P < 0.001$). Snowy egrets (*E. thula* (Molina, 1782)), great egrets (*Ardea alba* L., 1758), and little blue herons (*E. caerulea* (L., 1758)) landed more often at ponds that contained decoys resembling conspecifics. At the intraspecific level, all observed reddish egrets selected flocks with like-plumaged decoys. Our results suggest that plumage colouration is an attractant for species with similar plumage, but white plumage is not an attractant for all wading bird species. White plumage may facilitate flock formation in certain species but does not serve as a universal attractant for wading birds of varying plumage colouration and size.

Résumé : On a avancé l'hypothèse qui veut que le plumage blanc des ardéidés facilite la formation des volées. Nous avons fait quatre expériences à l'aide de leurres afin de déterminer les facteurs impliqués dans l'attirance des échassiers pour un étang particulier. Les trois premières expériences vérifient les effets de la coloration du plumage, de la taille de la volée et des leurres spécifiques à l'espèce sur la formation des volées. La quatrième expérience examine les différences intraspécifiques du choix de la volée chez deux morphes de couleurs différentes de l'aigrette roussâtre, *Egretta rufescens* (Gmelin, 1789). Les échassiers se posent plus fréquemment près de groupes de leurres que près de leurres isolés et que dans les sites sans leurres ($P < 0{,}001$); ils n'ont pas, cependant, d'attirance générale pour le plumage blanc ($P > 0{,}05$). Les espèces à plumage blanc sont attirées par les leurres blancs ($P < 0{,}001$) et celles à plumage foncé par les leurres foncés ($P < 0{,}001$). Les aigrettes neigeuses (*E. thula* (Molina, 1782)), les grandes aigrettes (*Ardea alba* L., 1758) et les aigrettes bleues (*E. caerulea* (L., 1758)) se posent plus souvent dans des étangs qui contiennent des leurres qui leur ressemblent. À l'échelle intraspécifique, toutes les aigrettes roussâtres ont choisi des groupes de leurres qui possèdent leur propre couleur de plumage. Nos résultats indiquent que la coloration du plumage attire les espèces de plumage semblable, mais que le plumage blanc n'attire pas toutes les espèces d'échassiers. Le plumage blanc peut faciliter la formation des volées chez certaines espèces, mais il n'attire pas de façon universelle tous les oiseaux échassiers qui varient en taille et en couleur de plumage.

[Traduit par la Rédaction]

Introduction

The adaptive value of colouration in animals has been debated and studied intensively (Huxley 1938; Hamilton 1973). Cryptic colouration is common in some species of birds, presumably for concealment — either protection from predators or crypsis to prey (Gill 1990). Lack of crypsis in birds is often associated with bright colouration in adults, which is used for mate attraction. In these mating systems, one sex is usually brightly coloured while the opposite sex is dull in colour. One exception to plumage colouration in birds is the occurrence of species with all-white plumage in both sexes.

White plumage, although not absent in other bird orders, is prevalent in many species of waterbirds (Tickell 2003). In the order Ciconiiformes, numerous groups of closely related species differ considerably in plumage colouration (dark versus white) (Sibley and Ahlquist 1990; Sheldon et al. 1995). Within the family Ardeidae, six species exhibit two distinct colour morphs (dichromatism), where an individual is either all white or dark-plumaged. Currently accepted phylogenies suggest that white plumage arose independently several times (Sibley and Ahlquist 1990; Sheldon et al. 1995). Numerous hypotheses for the adaptive significance of white plumage have been proposed, including crypsis to prey, thermoregulation, and sociality (Kushlan 1977; Ellis 1980; Mock 1980; Caldwell 1986; Tickell 2003). As part of an investigation into the ecological significance of white plumage (Green 2003), this study focused on the influence of white plumage on sociality in wading birds.

Received 21 October 2004. Accepted 28 April 2005. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 28 June 2005.

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 doi: 10.1139/Z05-058

Ciconiiformes often form large single- or mixed-species aggregations for both foraging and nesting. Foraging aggregations of wading birds may form for several reasons, including increased foraging success and reduced energy expenditure. Increased foraging success, or "positive interference" (see Mock 1980), refers to the situation where an individual's foraging efficiency is significantly enhanced by the presence of another forager. Foraging wading birds in flocks may experience reduced energy expenditure owing to a reduction in stepping rate (Kushlan 1978*a*) or the breakdown of territoriality (e.g., less energy expended chasing conspecifics; Wiggins 1991). The formation of bird aggregations may also occur for protection from predators. Flocking behaviour may enhance predator detection through shared vigilance or by a dilution or confusion effect on the predator (Hamilton 1971; Pulliam 1973). In Ardeidae, incidents of predation are scant and anecdotal (Monson 1951; Lowe 1954; Cottrille and Cottrille 1958), making it difficult to test whether predation is a major impetus for flocking in long-legged wading birds (Mock 1980; but see Caldwell 1986).

Kushlan (1977) suggested that white plumage functions as a signal for the formation of wading bird aggregations. He observed that significantly more wading birds were attracted to white decoys than to dark decoys, and he argued that white plumage might be a way of attracting other birds to foraging aggregations. All species attracted to the flocks were lumped together for the analysis and there was no discussion of which species (and hence plumage colours) were attracted to the white or dark flocks. Using snowy egret (*Egretta thula* (Molina, 1782)), great egret (*Ardea alba* L., 1758), and mixed flock (white and dark-plumaged birds) decoys, several studies (Caldwell 1981; Master 1992) have shown that snowy egrets are the "attractive force" in drawing in several species of herons, regardless of plumage colouration. However, these studies failed to offer flocks of dark-plumaged decoys as an alternative choice to incoming wading birds.

In this study, we examine the possible influences that plumage colouration may have on flock formation in Ciconiiformes. We test the hypothesis that white plumage is more attractive than dark plumage to wading birds of both plumage colourations. We examine the effects that flock size, species composition, and solar exposure (overcast versus full sun) may have on flock formation, as well as interactions of these effects with plumage colouration. Our results have implications for current flocking behaviour theory and contribute to our understanding of the role of plumage colouration in encouraging or suppressing sociality.

Materials and methods

Effect of plumage colouration and flock size

This experiment examined whether white plumage colouration and flock size were influential in attracting wading birds to an area. This research was conducted in experimental ponds at the University of Louisiana at Lafayette Crawfish Research Center near Cade, Louisiana. The ponds were part of a set of 17 replicate 0.3-ha impoundments. Water level, aquatic vegetation, and prey abundance were assumed to be similar among all impoundments. All ponds were drained annually in July and reflooded in October from the same water source (Bayou Teche).

Four sets of decoys and one control (no decoys) constituted the five treatments used in this experiment (Fig. 1). Our decoy sets were as follows: one great egret (white plumage), one great blue heron (*Ardea herodias* L., 1758; dark plumage), five great egrets, and five great blue herons. All decoys were commercially available, moulded plastic "heron" decoys of either great blue heron type or great egret type (Cabellas Sporting Goods, Inc.). These decoys were chosen because they were all similar in size, thereby controlling for any "size" choice made by wading birds. The experiment was conducted during April–May 2001.

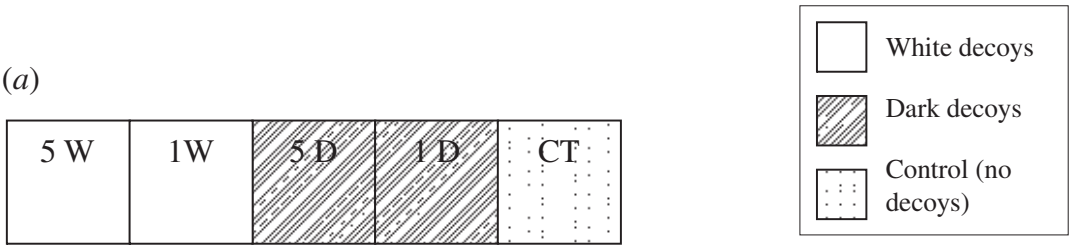
Each day, treatments were randomly assigned to five adjacent ponds. In the ponds assigned five decoys, the decoys were placed 1 m apart. The decoys were set up before sunrise on each observation day. The observation period began at local sunrise and ended approximately 2 h later (e.g., 0730 US Central Daylight Time (CDT) to 0930 CDT) or when regular arrivals of birds from night roosts diminished. The observer (M.C.G.) was situated on a levee perpendicular to the ponds, approximately 50 m from the closest pond. The observer monitored all ponds and recorded the species and time of arrival for each wading bird that landed in the ponds. Percent cloud cover was also recorded, as observations were grouped into "sunny" (<50% cloud cover) and "cloudy" (>50% cloud cover) days for analysis. Once the first bird had landed at one of the ponds, all birds were flushed from the area and the ponds were randomly assigned new treatments; no birds were present at the beginning of the next observation. Only the first bird arriving at a pond was used in the analysis. Species that had fewer than five individuals land at our ponds were dropped from our analyses.

We treated each landing by an individual bird as an independent observation. The Crawfish Research Center is located less than 16 km from several large rookeries (e.g., Lake Martin, >15 000 breeding pairs) and roost sites, resulting in high densities of wading birds flying over and landing at the research center (Martin and Lester 1990; M.C. Green, personal observation; J. Huner, personal communication). This high number of overflying wading birds presumably minimizes the chance of the same bird landing repeatedly at our ponds. Furthermore, because birds were flushed immediately upon landing, we assume that they had little inclination to repeatedly visit our experimental ponds. Pond depth was maintained at 15–17 cm in each pond and only shoreline vegetation was present in the ponds. Prey densities were unknown but were assumed to be equal. We assume that birds are unable to detect prey densities prior to landing at a pond (aerially). Therefore, because birds were flushed upon landing and decoy treatments were re-randomized after each landing, prey densities of our experimental ponds probably had little influence on choice of pond.

Statistical analyses were performed using the statistical software SAS® (SAS Institute Inc. 1999). Because multiple choices were available to a bird, we used log-linear modelling (PROC CATMOD) to test the null hypothesis of no association between flock size, plumage colouration, and solar condition. Log-linear modelling was also used to compare the choice of treatments between wading birds with white plumage (snowy egret; great egret; and white ibis,

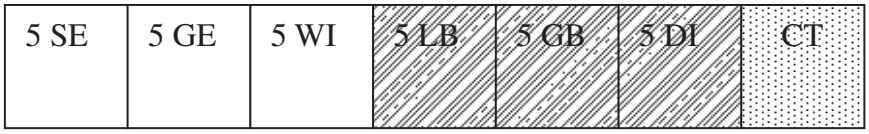
Fig. 1. Design of decoy experiments: (*a*) effect of plumage colouration and flock size; (*b*) effect of species-specific flocks; (*c*) effect of white plumage as an initial attractant; and (*d*) effect of plumage colouration and flock size on plumage dimorphic species. W, white-plumaged birds; D, dark-plumaged birds; CT, control (no decoys); GE, great egret, *Ardea alba*; SE, snowy egret, *Egretta thula*; WI, white ibis, *Eudocimus albus*; GB, great blue heron, *Ardea herodias*; LB, little blue heron, *Egretta caerulea*; and DI, white-faced ibis, *Plegadis chihi*. The number preceding an abbreviation represents the number of decoys used in that pond. Shading represents sub-groups used in some statistical analyses.

(*a*)



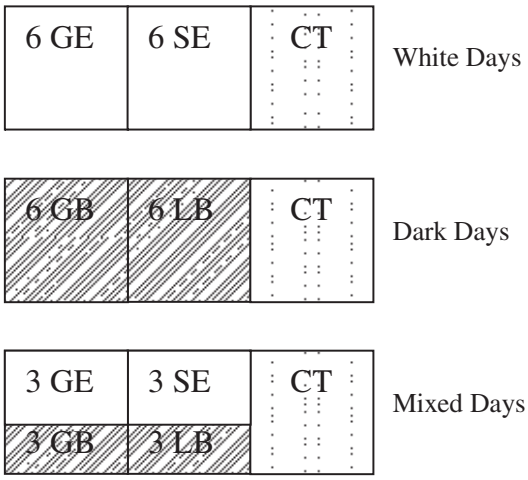
H_o: No association between pond choice, flock size, plumage colouration and solar condition (n=96).
H_o: No association between pond choice and plumage colouration (n=96).

(*b*)



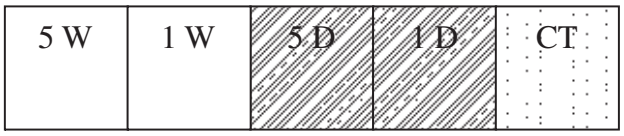
H_o: No association between pond choice, species, and plumage colouration (n=104).
H_o: No association between pond choice and plumage colouration (n=104).

(*c*)



H_o: No difference in number of birds (per species) landing at ponds between days (n=11 per treatment day).
H_o: No difference in choice of ponds (per species) within each treatment day (n=11 per treatment day).

(*d*)



H_o: No association between pond choice, flock size, plumage colouration and solar condition (n=18).
H_o: No association between pond choice and plumage colouration (n=18).

Eudocimus albus (L., 1758)) and wading birds with dark plumage (little blue heron, *Egretta caerulea* (L., 1758); great blue heron; and white-faced ibis, *Plegadis chihi* (Vieillot, 1817)). Factors were evaluated simultaneously to control for type I error rate. We hypothesized that wading birds, regardless of species and plumage colouration, would select the white "flock" over all other choices. We also hypothesized that white plumage would be more visible on clear days and, consequently, the magnitude of flock choice would be greater on clear days.

Effect of species-specific flocks

We conducted this experiment to examine whether a wading bird, given a choice of ponds that contained species-specific flocks, would select a pond with members of its own species or just birds with similar plumage colouration. For this experiment, seven ponds were used at the Crawfish Research Center with the following treatments: six species-specific "flocks", each containing five decoys, and one control (Fig. 1). The decoys were all commercially available (heron confidence decoy, Cabellas Sporting Goods, Inc.; yard flamingo, ArtLine, Inc.; curlew decoy, Knutson's Inc.) and were modified to resemble the following species: heron confidence decoys, great egret and great blue heron; yard flamingo decoys, snowy egret and little blue heron; and curlew decoys, white ibis and white-faced ibis. The experiment was conducted from April to May 2002.

The experiment was conducted and analysed in the same manner as the previous experiment testing plumage colouration and flock size (PROC CATMOD). We predicted that wading birds would land more often at one of the white flocks than at the dark flocks or the control if white plumage was the attractant. We also predicted that wading birds would land more often at their species-specific flock than at all other choices if they were attracted to their own species. We also conducted a χ^2 goodness-of-fit test to examine the hypothesis that each species distributed itself equally among the seven treatments.

Effect of white plumage as an initial attractant

Because the previous experiments contained both white and dark decoys, it was not clear whether responses to white decoys played a role in attracting birds to a group of ponds. For example, little blue herons might be attracted to a given area because of the presence of white plumage but, upon arrival, instead select the aggregation containing conspecifics. Therefore, we conducted an experiment to evaluate whether white plumage played a role in attracting birds to a given area. For this experiment, we used three treatments: "large heron" pond, "small heron" pond, and control (no decoys) (Fig. 1). Days were treated as observations, with each day a "white", "dark", or "mixed" flock day. On white days the following treatments were available: (*i*) six great egret decoys, (*ii*) six snowy egret decoys, and (*iii*) control with no decoys. On dark days, treatments consisted of (*i*) six great blue heron decoys, (*ii*) six little blue heron decoys, and (*iii*) control with no decoys. Treatments on mixed days consisted of (*i*) three great egrets and three great blue herons, (*ii*) three snowy egrets and three little blue herons, and (*iii*) control with no decoys. The experiment was conducted from April to May 2003.

The decoys were set up before sunrise on each observation day. The observation period began at sunrise and ended exactly 120 min afterwards (approximately 0900). Once the first bird had landed at one of the ponds, all birds were flushed from the area and the ponds were randomly assigned new treatments. Only the first bird arriving at a pond was used in the analysis.

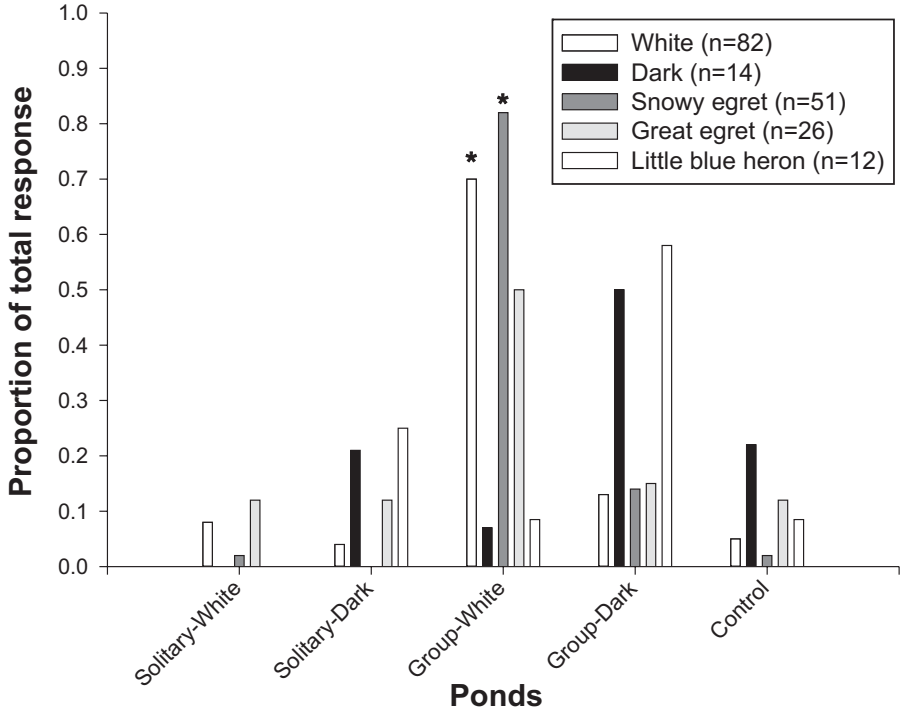
Statistical analyses were performed using the statistical software SAS® (SAS Institute Inc. 1999). We used the Kruskal–Wallis test (PROC NPAR1WAY) to assess wading bird species' responses to specific plumage colouration across treatments (white, dark, or mixed days). We used the Nemenyi test for nonparametric multiple comparisons between treatments with $\alpha = 0.05$ (Zar 1996); this test controls for experiment-wise error rate. To assess wading bird species' responses to specific sizes of decoys (large, small, or control) within a treatment day, we used Friedman's test, a nonparametric test for a randomized block design. The Nemenyi test was again used for post-hoc nonparametric multiple comparisons between treatments (Zar 1996). Analyses were conducted for only three species: great egret, snowy egret, and little blue heron. No other wading bird species landed at the ponds in numbers sufficient to warrant analysis. The dependent variable in the models was the number of birds that landed at the ponds on each day; decoy size and plumage colouration were the independent variables. We predicted that if wading birds preferred white plumage, they would land at ponds more often on days with some number of white decoys than on days without white decoys (i.e., birds would land more often on white and mixed days), regardless of their own plumage colouration. Furthermore, we predicted that if wading birds preferred their own species, they would land at ponds more often on days with decoys resembling conspecifics (e.g., snowy egrets would land more often on white and mixed days). We also predicted that species would land more often at the pond containing like-sized members than at other ponds (e.g., snowy egrets would land more often at the small heron pond).

Effect of plumage colouration and flock size on plumage dimorphic species

Comparing the responses of individuals between species confounds the effect of plumage colour on sociality with preferences for members of the same species. Therefore, we conducted an experiment to test the flock preference of both colour morphs of reddish egrets, *Egretta rufescens* (Gmelin, 1789). This experiment was conducted at Laguna Atascosa National Wildlife Refuge near Rio Hondo, Texas. Both colour morphs of reddish egrets were abundant, and ratios of white to dark morphs approached 1:1. The experiment was conducted on several tidal flats on the refuge, alternating between the flats on the basis of seasonal use by reddish egrets. Water level, aquatic vegetation, and prey abundance were assumed to be similar among all flats because they shared the same body of water.

Four sets of decoys and one control (no decoys) were used as the five treatments in this experiment (Fig. 1). All decoys were commercially available, moulded plastic heron confi-

Fig. 2. Responses of white birds (great egrets and snowy egrets), dark birds (white-faced ibis and little blue herons), snowy egrets, great egrets, and little blue herons to five decoy treatments involving plumage colouration (white or dark) and flock size (solitary or group), using log-linear modelling. Responses to decoy treatments are presented as proportions of the total number of landings observed for a particular species or pair of species. An asterisk indicates that the response to a treatment was significantly different from the responses to other treatments at the $\alpha = 0.05$ level.



dence decoys (Knutson's Inc.) modified to look like either white or dark morphs of reddish egrets. These decoys are smaller than Cabellas' heron confidence decoys and closer in size to reddish egrets. The four decoy sets were as follows: one reddish egret (white morph), one reddish egret (dark morph), five reddish egrets (white), and five reddish egrets (dark). The experiment was conducted in June of 2002 and 2003. Five 10 m × 10 m areas were laid out with flagging and used to demarcate the five treatment sites. Treatments were placed 30 m apart to provide clear separation between treatments. After each landing, birds were flushed and treatments were randomly reassigned among the five adjacent plots. In the plots assigned five decoys, the decoys were placed 1 m apart.

We analysed these data using Fisher's exact test (PROC FREQ, SAS Institute Inc. 1999). We tested the hypothesis that the choice of flock colour was independent of the two colour morphs of the reddish egret. We hypothesized that reddish egrets, regardless of their own plumage colouration, would select the flock containing white plumage over all other choices.

Results

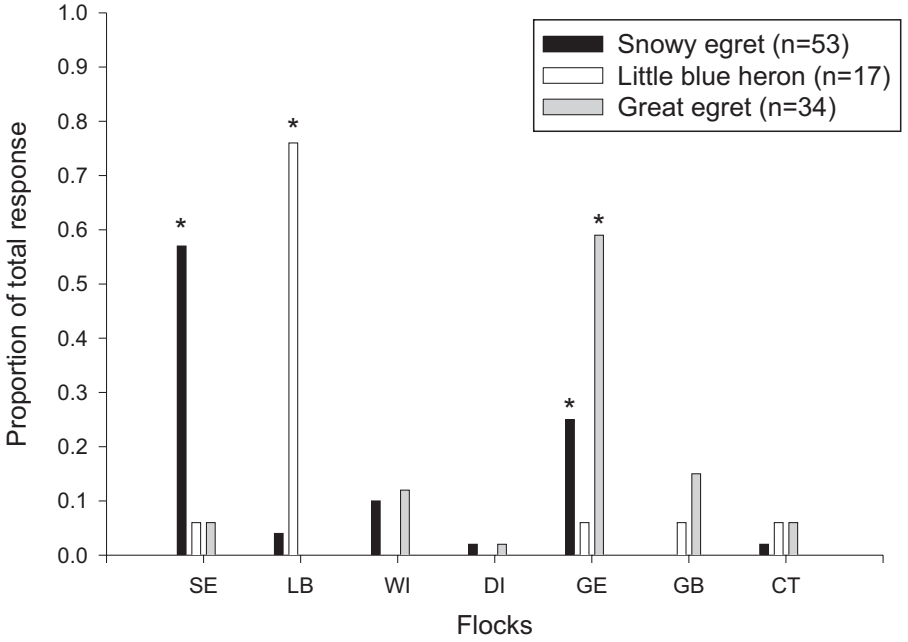
Effect of plumage colouration and flock size

There was no main effect of plumage colouration on flock choice, as wading birds (all species pooled) selected ponds with decoys of either colour ($\chi^2_1 = 0.1$, $P = 0.74$). There was no effect of pond on wading bird choice of treatments ($\chi^2_4 = 2.7$, $P = 0.61$), indicating that our results were not influenced by characteristics of the ponds. Wading birds selected ponds with flocks more often than ponds with one or no decoys ($\chi^2_2 = 32.19$, $P < 0.001$; Fig. 2). There was no difference in choice of treatments by wading birds between cloudy and sunny days ($\chi^2_1 = 0.6$, $P = 0.57$). There was a difference between white- and dark-plumaged birds in choice of treatments ($\chi^2_1 = 10.1$, $P < 0.01$), as white-plumaged birds chose white flocks ($\chi^2_1 = 10.4$, $P < 0.001$) and dark-plumaged birds chose dark flocks ($\chi^2_1 = 10.4$, $P < 0.001$) over all other treatments. Snowy egrets preferred white flocks ($\chi^2_1 = 15.7$, $P < 0.001$), whereas little blue herons tended to select dark decoys, although this difference was not statistically significant ($\chi^2_1 = 3.4$, $P = 0.07$). All little blue herons observed in our experiments were dark-plumaged adults. No other species showed any particular preference for a treatment.

Effect of species-specific flocks

Wading birds differentially selected certain flocks over other treatments ($\chi^2_6 = 16.4$, $P = 0.01$; Fig. 3). There was no effect of pond on wading bird choice of decoy treatments ($\chi^2_6 = 11.3$, $P = 0.08$). Different species of participating wading birds also selected different treatments ($\chi^2_4 = 23.4$, $P < 0.001$). Great egrets ($\chi^2_5 = 45.4$, $P < 0.001$) and little blue herons ($\chi^2_5 = 33.9$, $P < 0.001$) preferred their species-specific flock to all other choices. Snowy egrets preferred both their own species-specific flock and the great egret flock to all other treatments ($\chi^2_5 = 72.8$, $P < 0.001$). No other flock selection or species choice was significant. Although we used both white ibis and white-faced ibis decoys

Fig. 3. Responses of snowy egrets, little blue herons, and great egrets to seven treatments containing species-specific "flocks" of decoys, using log-linear modelling. Treatments are as follows: SE, snowy egret; LB, little blue heron; WI, white ibis; DI, dark ibis; GE, great egret; GB, great blue heron; and CT, control. Responses to treatments are presented as proportions of the total number of landings observed for a particular species. An asterisk indicates that a response to a treatment was significantly different from the responses to other treatments at the $\alpha = 0.05$ level.



in our treatments, no species of ibis was attracted to any pond and no species preferred either treatment containing ibis decoys.

Effect of white plumage as an initial attractant

Wading birds differed in their response to the three flock compositions offered. Snowy egrets landed at ponds more often on white and mixed flock days than on dark flock days ($\chi^2_2 = 11.2$, $P < 0.001$; Fig. 4). There was no difference in the response of snowy egrets between white and mixed flock days or between mixed and dark flock days. However, snowy egrets landed more often on white flock days than on dark flock days. Great egrets also landed at ponds more often on white and mixed flock days than on dark flock days ($\chi^2_2 = 9.7$, $P = 0.01$). They were similarly attracted to ponds on white and mixed flock days and on mixed and dark flock days, but were more attracted to ponds on white flock days than on dark flock days. Little blue herons did not exhibit any tendency to land at ponds on a specific flock day ($\chi^2_2 = 2.4$, $P = 0.38$).

Within each day, wading birds differed in their attraction to varying sizes of decoys (Fig. 5). On white and mixed flock days, the number of landings of snowy egrets significantly differed among the decoy size treatments ($\chi^2_2 = 13.1$, $P < 0.05$). Snowy egrets landed at the pond with the size class resembling snowy egrets more often than the pond with the size class representing larger herons or egrets or the control pond. There was no difference in their avoidance of ponds with the large heron size class and control ponds. Great egrets exhibited similar discrimination in their choice of a pond with a particular decoy size class on white and mixed flock days ($\chi^2_2 = 9.8$, $P < 0.05$). The pond with the large size class was selected more often by great egrets than the pond with the small size class and the control pond. Great egrets exhibited no difference in their degree of attraction to the pond with the small size class or the control pond. Little blue herons exhibited a size preference on mixed and dark flock days ($\chi^2_2 = 6.82$, $P < 0.05$). Although the size preference was statistically significant for little blue herons, the more conservative multiple comparisons test revealed no significant differences between the size classes.

Effect of plumage colouration and flock size on plumage dimorphic species

Reddish egret morphs differed significantly in their choice of flock colour ($P < 0.001$, Fig. 6). Dark-morph reddish egrets significantly preferred dark decoy(s) and white morphs significantly preferred white decoy(s). All white morphs analysed landed at the white flock, while 67% of dark morphs landed at the dark flock and 33% of dark morphs landed at the solitary dark decoy.

Discussion

Effect of plumage colouration and flock size

Modified commercially available decoys worked well in attracting wading birds to a given area (Crozier and Gawlik 2003; Heath and Frederick 2003). As a whole, herons and egrets were attracted to ponds with decoys over ponds without decoys. Furthermore, white and dark birds were attracted to flocks over solitary decoys. White plumage has been suggested to be important in attracting herons to a particular area (Armstrong 1971; Kushlan 1977; Caldwell 1986; Beauchamp and Heeb 2001). Our results suggest that white plumage may not play an important role in attracting all herons, as previously hypothesized. While white-plumaged de-

Fig. 4. Box plots of number of choices (landings) per treatment day for great egrets, snowy egrets, and little blue herons, using the Kruskal–Wallis test. Treatment days comprised white (n = 11), mixed (n = 11), and dark flock days (n = 11). The box boundary closest to zero indicates the 25th percentile, the line within the box marks the median, and the box boundary farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles. Treatments with the same letter above the box were not significantly different from one another based on the Nemenyi test (Zar 1996).

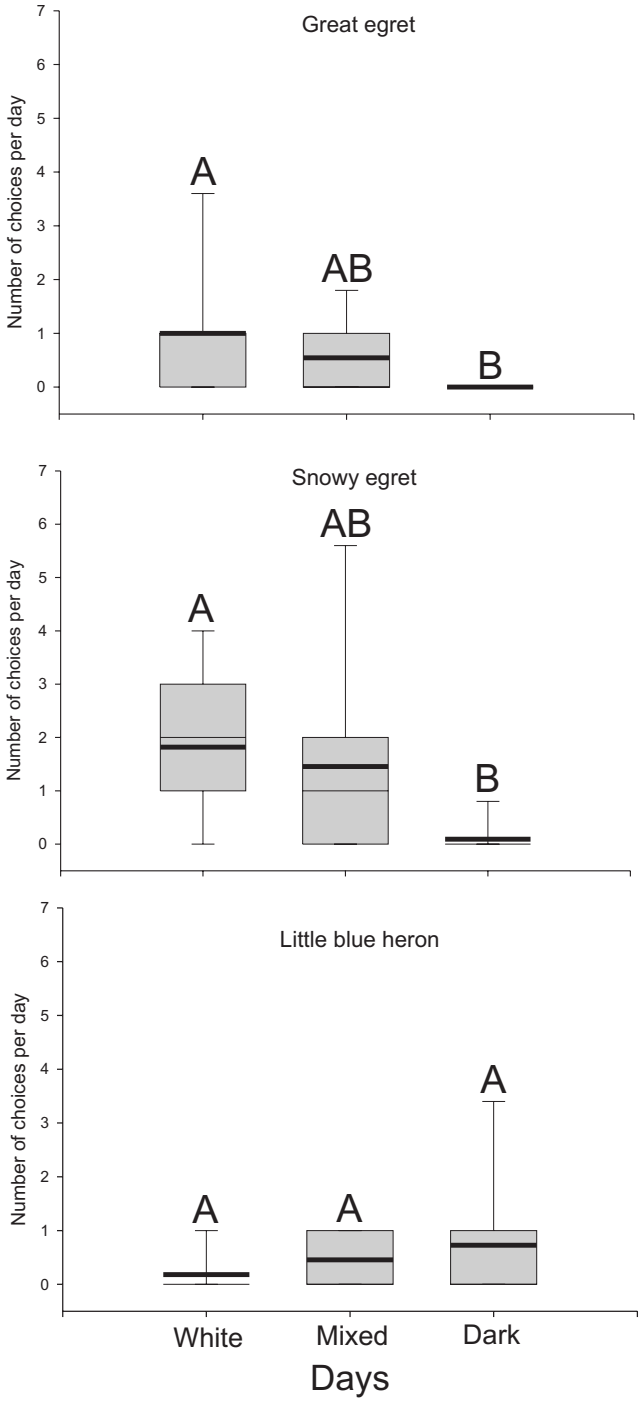
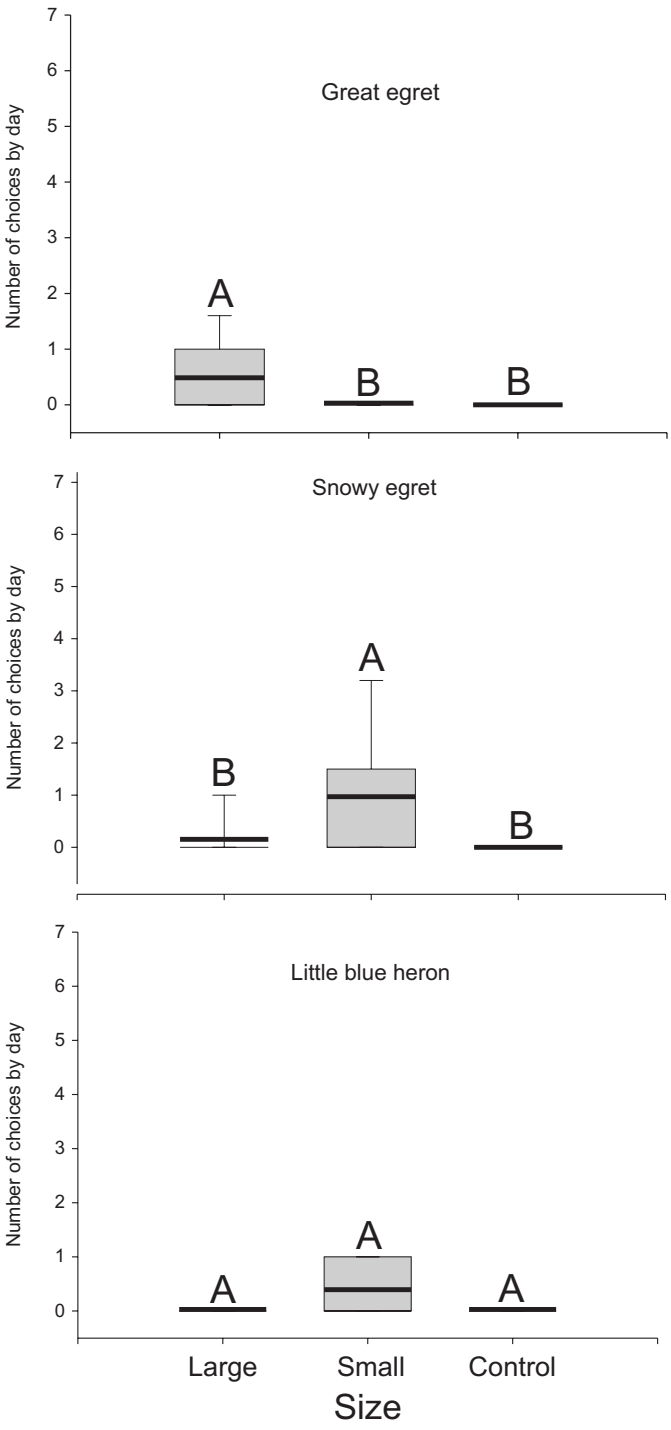
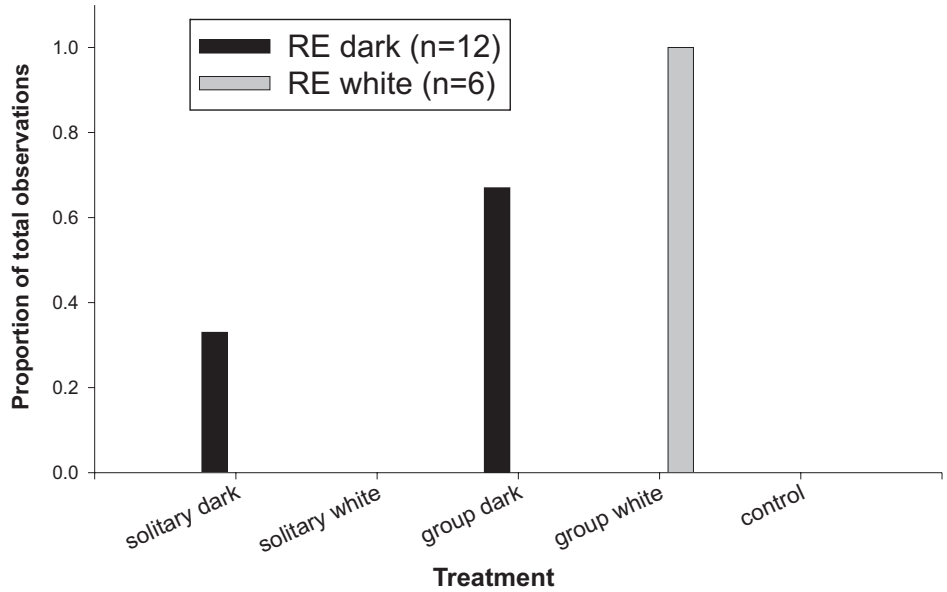


Fig. 5. Box plots of number of choices (landings) per day (n = 33) for great egrets, snowy egrets, and little blue herons, using the Kruskal–Wallis test. Treatments comprised "large heron" flocks, "small heron" flocks, and control (no decoys). For details, see Fig. 4. Treatments with the same letter above the box were not significantly different from one another based on the Nemenyi test (Zar 1996).



coys were selected in a majority of the observations, over 80% of the herons participating in the experiment were white-plumaged. Dark birds, when participating in our experiment, selected the dark-plumaged decoys over the white-plumaged decoys. White plumage has also been suggested to be more conspicuous, and therefore more attractive

Fig. 6. Responses of colour morphs of reddish egrets, *Egretta rufescens* (RE), to five decoy treatments involving plumage colouration (white or dark) and flock size (solitary or dark), using Fisher's exact test. Responses are presented as proportions of the total number of landings observed for each colour morph.



to wading birds, on overcast days (Kushlan 1977). We found no support for the idea that white plumage attracts more wading birds than dark plumage on cloudy days. However, our two categories of relative cloud cover did not accommodate the full range of ambient light conditions. It is possible that finer partitioning of observations might have revealed differences in attractiveness under different light conditions.

Effects of species-specific flocks

The results from this experiment suggest that wading birds were attracted to ponds containing conspecifics over congenerics and other species of Ciconiiformes. Our study does not support the hypothesis that certain wading bird species (e.g., snowy egret) attract other species of wading birds and thus serve as founder species for flocks (Caldwell 1981; Master 1992; Gawlik 2003).

Effect of white plumage as an initial attractant

In our experiment using white plumage as an initial attractant, days with white decoys attracted significantly more white-plumaged birds (great egrets, snowy egrets), while days with dark decoys attracted more dark-plumaged birds (little blue herons). Within each treatment day, great egrets, snowy egrets, and little blue herons preferred ponds containing decoys of similar size to themselves. Our results suggest that wading birds prefer to land next to birds with plumage colouration and size similar to their own.

Interspecific comparisons

For our first three experiments, only three species, great egret, snowy egret, and little blue heron, participated in sufficient numbers for us to make inferences concerning attraction to flocks. Although we also targeted great blue herons in our experiments, we observed a small response from this species, presumably because of its typical asocial behaviour. This species is considered to be less gregarious than most heron species, and our results provide support for this idea (Butler 1992).

Great egrets exhibit seasonal territoriality, and some studies suggest that this species may often avoid foraging near conspecifics rather than join a conspecific flock (Wiggins 1991; Smith 1995). However, in the species-specific flock experiment and the white plumage as an initial attractant experiment, great egrets selected conspecific flocks over all other choices. For great egrets, these results are different from those of the plumage colouration and flock size experiment, where great egrets showed no attraction to any particular flock. However, the decoys in the plumage colouration and flock size experiment were the commercially available "heron" decoys not painted (modified) to resemble any particular species. In the species-specific experiment, we painted all decoys to resemble the six target species. Great egrets appeared to detect these differences in the decoys and were significantly more attracted to the conspecific decoys.

Snowy egrets were the only white-plumaged birds to exhibit a strong preference for the white flock in our plumage colouration and flock size experiment. Master et al. (1993) suggested that snowy egrets are actually dependent upon social foraging for increased foraging success. When presented with species-specific decoys in our second experiment, snowy egrets again exhibited preference towards white birds, selecting white-plumaged decoys (snowy egret, great egret, and white ibis) in over 92% of our observations. Although snowy egrets preferred flocks of their own species 2:1 over the great egret flock, both snowy egret and great egret flocks were significantly preferred over the other treatments. Our results for snowy egrets are consistent with earlier experiments in that this species exhibited strong preferences for white plumage and "little" decoys (e.g., snowy egrets). These results provide further evidence of snowy egrets' possible dependence on social foraging (Caldwell 1981; Master et al. 1993). Snowy egrets are also considered to be excellent indicators of locations of abundant prey (Caldwell 1979,

1981). Because of this, it has been suggested that snowy egrets initiate flocking and serve as an attractant to other wading birds forming mixed-species flocks (Caldwell 1981; Master 1992). We found no evidence that snowy egret decoys attracted significant numbers of herons other than snowy egrets themselves.

Both the plumage colouration and flock size experiment and the species-specific flock experiment suggest that little blue herons were significantly more attracted to dark decoys and, when given a choice, species-specific decoys. Caldwell (1981) observed significantly more little blue herons attracted to snowy egret decoys than mixed-species decoys and concluded that little blue herons prefer snowy egret flocks. Our results contradict her findings, because we found that little blue herons exhibited a strong preference for conspecific flocks over snowy egrets, as well as other types. Caldwell (1981) did not "offer" a little blue heron flock and instead had only a mixed-species flock in which only two of five decoys were dark-plumaged, which may explain her failure to detect an attraction to dark decoys. In our third experiment examining white plumage as an initial attractant, little blue herons did not show significant preferences for a particular colour. This, however, was presumably a product of sample size, as only 15 birds participated in the experiment and over 86% of these individuals landed at ponds containing little blue heron decoys (dark days, 8; mixed days, 5; white days, 2). However, all birds landing at ponds on dark or mixed days landed at the ponds containing the small-size-class decoys. Little blue herons, considered less gregarious than snowy egrets and great egrets, may have participated less in our experiments because of the infrequent occurrence of little blue heron flocks in nature. However, previous findings suggesting that little blue herons are attracted to snowy egret flocks (e.g., Caldwell 1981) were not supported by our experiments. Less than 7% (2 of 29 birds) of little blue herons landed at the pond containing snowy egret decoys in our first two experiments.

Effect of plumage colouration and flock size on plumage dimorphic species

Reddish egrets exhibited strong preferences for like-plumaged decoys, as all participating birds landed at decoys sharing their plumage colouration. While white-morph reddish egrets preferred white flocks, dark-morph reddish egrets preferred both dark solitary birds and dark flocks. Although considered less gregarious than most birds in the family Ardeidae (Kushlan 1978*b*), reddish egrets exhibited social tendencies typical of more gregarious species. Farmer (1991) and Lowther and Paul (2002) reported reddish egrets in south Texas to be more gregarious than other Gulf coastal populations. Our results are more consistent with these studies that support gregariousness in reddish egrets.

Our results suggest that given a choice of flocks with like plumage and contrasting plumage, reddish egrets are attracted to their own plumage colouration. The advantages of joining a like-plumaged flock are unclear. Reddish egrets generally forage solitarily and exhibit territoriality but may join mixed-species flocks when prey reach some level of abundance (Lowther and Paul 2002). Reddish egrets were also reported to occasionally form species-specific flocks for both foraging and loafing (Farmer 1991); however, the proportion of white:dark morphs in these species-specific flocks was not reported. In our experiment, decoys were placed in areas devoid of foraging birds to control for factors (e.g., abundant prey resources) other than flock size and colour. Reddish egrets may have selected like-plumaged flocks over other choices to minimize the odd prey effect, where predators single out more conspicuous individuals in a group (Mueller 1975). While predation upon reddish egrets is rarely observed (Lowther and Paul 2002), peregrine falcons (*Falco peregrinus* Tunstall, 1771) and coyote (*Canis latrans* Say, 1823) were commonly seen on the tidal flats of our study site.

On being "white"

Our results are inconsistent with other studies on the "attractiveness" of white plumage to social wading birds. We suggest that white plumage plays an important role in attracting white wading birds and not necessarily dark-plumaged wading birds to an area. Dark plumage appears to play its own important role in attracting certain species of wading birds to a given area. Our results suggest that herons are attracted to flocks containing like-plumaged and like-sized birds.

White plumage, through its conspicuousness, may act as a signal informing other birds when a particular area or territory is occupied (Payne and Risley 1976; Mock 1980). White plumage may minimize "active defence" of a territory by signalling to would-be interlopers that an area is already taken. This explanation seems plausible considering the territorial behaviour commonly seen in great egrets. However, our results show that great egrets were consistently attracted to our great egret decoys rather than repelled. We did sometimes observe "territorial" behaviour from incoming great egrets, where the birds would fly low over the decoys, emitting territorial aggression calls (Maccarone and Parsons 1994). These behaviours were less frequent, however, than those of birds that chose to land at the decoys, indicating that herons preferred flocks. Snowy egrets and white ibis, both highly gregarious, are considered social foragers and are regularly found in the presence of other wading birds (Master 1992; Smith 1995). White plumage may serve to facilitate the formation of flocks but it is debatable whether or not flock members actually benefit from the presence of neighbours. Studies demonstrating the benefits of group foraging for wading birds are not consistent between species (see Mock 1980). Flock formations in wading birds are often attributed to drawdowns or pooling of prey (Kushlan 1976). While white plumage may attract birds to a particular area, it seems that conspicuousness (e.g., white plumage) would actually be a disadvantage in such situations (e.g., increased competition from neighbours).

Conclusions

We suggest that although white plumage may serve to attract herons to a particular area, it appears most effective at attracting white-plumaged birds. Likewise, dark plumage appears to effectively attract dark-plumaged birds. For the interspecific comparisons, our results suggest that flocks of one's own species may signal to the overflying individual that resources are available. Our intraspecific experiment with reddish egrets suggests that within a dimorphic species,

birds go beyond the attraction to species-specific flocks and are attracted to like-plumaged and like-sized individuals. Our results with reddish egrets suggest that even within a dimorphic species, where colour morphs frequently associate with one another (e.g., nesting, foraging), birds, when given a choice, flock with other birds that are similar in appearance. While this may signal available resources to the overflying individual, it is also plausible that reddish egrets select like-plumaged flocks to minimize the chance of being the odd individual in case of a predation event. White plumage may facilitate flock formation in white-plumaged species or colour morphs but does not serve as a universal attractant to wading birds of varying plumage colouration and size.

Acknowledgements

We thank J. Huner and the University of Louisiana at Lafayette Crawfish Research Center, as well as L. Laack, M. Fernandez, and Laguna Atascosa National Wildlife Refuge, for use of their facilities. Our research was partially funded by the Waterbird Society Grant in Ciconiiform Biology and Conservation, Sigma Xi Grants-In-Aid of Research, and University of Louisiana at Lafayette Graduate Student Organization. We thank D.F. Westneat and two anonymous reviewers for suggestions on an earlier version of this manuscript.

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