



Influence of plumage colour on prey response: does habitat alter heron crypsis to prey?

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The foraging strategies of wading birds may be influenced by their degree of crypsis to aquatic prey. White plumage has been hypothesized to be adaptive for herons hunting in open water habitats. We tested this hypothesis with laboratory and field experiments with multiple prey species. We investigated the response of crayfish, *Procambarus* spp., and mosquitofish, *Gambusia affinis*, to white- and dark-plumaged birds in an experimental chamber. We compared the time spent by a prey in front of a snowy egret, *Egretta thula*, mount, little blue heron, *E. caerulea*, mount, and a control (dowel) with and without backdrop vegetation. Mosquitofish tended to spend less time under the little blue heron mount with no backdrop present but made no observable response to either plumage colour against a vegetative backdrop. We assessed prey response in the field using three drop traps. Each trap had either a little blue heron mount, a snowy egret mount or a control (dowel) mounted underneath a trap. We compared the amount of biomass captured between treatments. More prey biomass (mosquitofish, crayfish and anurans) was captured under the control and snowy egret treatments than under the little blue heron treatment. Our results suggest that dark plumage may be a disadvantage to herons foraging in open water. In vegetation, structural complexity of the habitat appears to nullify differences in plumage colour between white and dark foraging herons.

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White plumage has apparently evolved independently numerous times in the order Ciconiiformes (Sibley & Ahlquist 1990; Sheldon et al. 1995). The evolution of white plumage has long intrigued biologists, resulting in numerous hypotheses for this phenomenon (Murton 1971; Kushlan 1978; Mock 1980; Caldwell 1986; Tickell 2003). One hypothesis suggests that white plumage may result in increased crypsis to aquatic prey (Thayer 1909; Meyerriecks 1960; Mock 1980; Gotmark 1987). The visual conspicuousness of a wading bird to aquatic prey may influence its foraging behaviour and success. White plumage may be more visually inconspicuous than dark plumage to aquatic prey against a bright background (e.g. clear skies). Conversely, dark plumage may be more cryptic to aquatic prey against a dark background (e.g. emergent or shoreline vegetation). Using adult (dark) and juvenile (white) little blue heron, *Egretta caerulea*, study skins, Mock (1980) observed more prey captured under traps with white mounts than under traps with dark mounts in open water. Crypsis to prey in

vegetated habitats was not analysed. Crypsis of white plumage to aquatic prey has also been shown in gulls (Gotmark 1987). Black-headed gulls, *Larus ridibundus*, with belly feathers dyed black capture significantly fewer prey than do black-headed gulls with normal white underparts.

The influence of plumage colour on prey selection may be supported by food habit studies. Recher (1972) reported that dark birds (little blue heron) prey upon bottom-dwelling fish, but white birds (snowy egret, *E. thula*) prey upon schooling fish. White plumage may confer an advantage to piscivorous birds in general (Phillips 1962; Mock 1980). Dark-plumaged birds may alter prey selection to less visually oriented species, such as crustaceans. In Florida, poecilids constitute the majority of prey in the diet of white-plumaged birds such as great egrets, *Ardea alba*, and snowy egrets, but dark-plumaged birds, such as little blue herons, forage primarily on crustaceans, with poecilids being of secondary importance (Smith 1997).

Great egrets and little blue herons may forage opportunistically, altering prey selection as hydrology and habitat conditions change (Smith 1997). This strategy may result from different prey use, based on the interaction between changes in crypsis caused by changes in water depth and the visibility of herons to particular prey. Smith (1997)

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reported that snowy egrets and tricoloured herons, *E. tricolor*, forage on similar prey but switch foraging strategies and tactics as changes in water levels occur.

In this study, we examined the possible influences of plumage colour and vegetation on the crypsis of wading birds to aquatic prey. We quantified the spectral reflectance of white (snowy egret) and blue (little blue heron) feathers to evaluate whether they differed from each other and from a vegetative backdrop of *Juncus romerianus*, a typical freshwater emergent marsh plant. We tested the hypotheses that white plumage is more cryptic to aquatic prey in open water and that dark plumage is more cryptic against a dark backdrop or vegetation to aquatic prey. We also examined the responses of several aquatic organisms, crayfish, *Procambarus* spp., and mosquitofish, *Gambusia affinis*, which are common prey items for herons. We discuss our results in light of current foraging theory and the role of plumage colour in the response of aquatic prey.

METHODS

Quantification of Spectral Reflectance

We quantified the spectral reflectance of one white feather from a snowy egret and one blue retrace feather from a little blue heron. We also measured the reflectance of living ('green') and senesced ('brown') portions of *J. romerianus*. We measured the spectral reflectance using a StellarNet model EPP2000 spectrometer. The light source used was a 150-W xenon lamp (Model 66056) from Oriel Instruments, with the substrates illuminated at 20° off horizontal illumination. Reflectance values are relative to a 99% (300–750 nm) Oriel Instruments white spectral calibration standard (Model 70496).

Laboratory Studies: Effects of Plumage Colour and Habitat

We collected 351 adult female mosquitofish and 300 adult crayfish (both sexes) from rice-crayfish aquaculture ponds at the University of Louisiana at Lafayette Crawfish Research Center near Cade, Louisiana, U.S.A. Prey species were captured within 3 days of experimental testing, housed in aquaria and subsequently released back into crayfish ponds upon completion of the experiments. We collected two snowy egrets and two little blue herons for study skin mounts under the Louisiana Department of Wildlife and Fisheries Scientific Collecting Permit LNHP-03-061 issued to the U.S. Geological Survey National Wetlands Research Center.

We investigated prey response to white- and dark-plumaged birds under laboratory conditions using skin mounts of little blue herons and snowy egrets. We tested the responses of two common prey species, mosquitofish and crayfish, to white and dark birds with and without a vegetative backdrop. In experiment 1, conducted in summer 2003, we tested the response of prey species to plumage colour in open water (no vegetative backdrop). We predicted that prey would spend less time in front of

the little blue heron mount than in front of the snowy egret mount. In experiment 2, conducted in summer 2004, we tested the responses of both prey species to plumage colour with vegetative backdrop and without (open water). Mosquitofish and crayfish differ in their visual acuity. Mosquitofish have paired, image-forming eyes that discriminate hues, brightness and contrasts; crayfish have compound eyes, limiting them to short-distance vision (Land 1981; Guthrie 1986). Based on these differences in vision, we also predicted that mosquitofish would respond more strongly to each treatment by spending less time in front of the conspicuous mount than would crayfish.

The two laboratory experiments were conducted in a greenhouse at the University of Louisiana at Lafayette Center for Ecology and Environmental Technology (CEET) under natural lighting conditions. The experimental chamber (178 × 70 × 13 cm) contained 10 cm of water. Water depth was shallow to minimize vertical movement of prey in the aquarium. A bird mount, either little blue heron or snowy egret, was placed on one end of the chamber; the side was randomly determined before each trial. For the control treatment, we used a dowel in place of a study skin mount. The prey, either a mosquitofish or a crayfish, was placed in an opaque capsule (PVC cap) in the centre of the experimental chamber, rendering the prey unable to see the mount while in the capsule. The capsule was raised and the response of the prey was recorded. We used a mounted video camera on one side of the chamber to record all responses. A dummy video camera was mounted on the opposite side to control for any possible side preferences influenced by the camera's position. The length of the chamber was divided into three equal sections. We recorded the location of the prey for 1 min, divided into three responses: towards, middle and away from mount, based on the three equal sections of the chamber. The response variable was the time (s) that the prey spent in front of the mount. No individual prey was used more than once in any experiment. We conducted trials using both prey species and with and without the presence of vegetation. We performed a Savage one-way test to examine the effects of plumage colour and vegetation on time spent in front of the mount (PROC NPAR1WAY, 1999, SAS Institute, Cary, North Carolina).

Field Study: Effects of Plumage Colour and Habitat

We investigated prey response to white- and dark-plumaged birds under field conditions using study skin mounts of little blue herons and snowy egrets. We conducted this experiment at the University of Louisiana at Lafayette Crawfish Research Center near Cade, Louisiana during the months of May–June, 2001–2003. We used a drop trap design modified from Kahl (1963) and Mock (1980), consisting of a PVC frame supporting a 60-cm metal cylinder, approximately the strike radius of a small heron/egret (Mock 1980). The drop traps were built during May 2001 and remained in place for the duration of the

experiment. This was done so that the traps were not novel objects in the water to the prey species; therefore, only the study skin mounts and dowels were novel to the prey. Three drop traps, placed 3 m apart in a 0.2-ha crayfish pond, were used. Drop traps were randomly assigned one of the following mounts for each trial: snowy egret, little blue heron or control (a dowel). Upon placement, these traps remained undisturbed for 30 min. After 30 min, the cylinders were dropped simultaneously and all captured prey was identified, counted and weighed. Trials were conducted during midday sun (clear to partly cloudy days) to minimize sun angle and no more than four trials were conducted per day.

To evaluate the effects of habitat on crypsis, treatments took place in either open (unvegetated) or vegetated (*J. roemerianus*) portions of the experimental pond. We used the Friedman test to analyse the effects of plumage colour on amount of biomass captured under each treatment (Conover 1980). We used the *F* approximation to determine significance at $\alpha = 0.05$, because of evidence that the chi-square approximation is undesirably conservative (Iman & Davenport 1980). We compared total biomass between the three treatments, as well as biomass from the three most prevalent prey species, mosquitofish, crayfish and tadpole/frog. In 2001 and 2002, we did not control for water turbidity, but in 2003, we installed a boardwalk over the pond to minimize disturbance of the water. We blocked by trial in our analysis to control for effects of daily and annual changes in water turbidity on our results. No comparison was made between blocks.

RESULTS

Quantification of Spectral Reflectance

The spectral reflectance of a snowy egret's white rectrice feather was high in the visible light range, with peak reflectance near 60% (Fig. 1). The little blue heron feather's reflectance was considerably less, with no reflectance

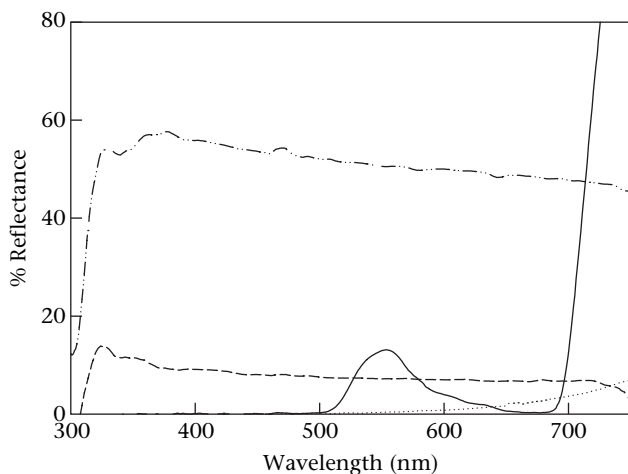


Figure 1. Percentage of spectral reflectance for rectrice feathers from snowy egret (— · —) and little blue heron (---) and living (—) and senesced (·····) plant tissue from *Juncus roemerianus*.

in the visible light range greater than 9%. The white and blue feathers were also reflected in the ultraviolet range (310–400 nm). The living plant tissue peaked around 550–560 nm (13% reflectivity), and the senesced plant tissue had the greatest reflectance in the longer wavelengths of visible light (600–700 nm).

Laboratory Studies: Effects of Plumage Coloration and Habitat

In experiment 1, with no vegetative backdrop, mosquitofish tended to spend the least time in front of the little blue heron (chi-square test: $\chi^2_2 = 5.514$, $P = 0.063$; Fig. 2). Crayfish did not respond differently to plumage colour and the control ($\chi^2_2 = 1.521$, $P = 0.468$; Fig. 2). In experiment 2, there was no significant difference between the responses to plumage colour and vegetation by mosquitofish ($\chi^2_2 = 1.271$, $P = 0.736$; Fig. 3a) and crayfish ($\chi^2_2 = 3.14$, $P = 0.675$; Fig. 3b). There was no significant difference between the responses of prey to plumage colour in either open water (mosquitofish: $\chi^2_2 = 3.00$, $P = 0.224$; crayfish: $\chi^2_2 = 1.27$, $P = 0.529$) or vegetation (mosquitofish: $\chi^2_2 = 1.17$, $P = 0.556$; crayfish: $\chi^2_2 = 0.96$, $P = 0.618$).

Field Studies: Effects of Plumage Colour and Habitat

We captured less total prey biomass with the little blue heron mount than in the other treatments (Friedman test: $T_2 = 2.23$, $0.05 < P < 0.10$); this difference was strongest in open water ($T_2 = 4.101$, $0.01 < P < 0.025$; Fig. 4). In vegetation, there was no significant difference between treatments in total biomass captured ($T_2 = 0.015$, $P > 0.20$). There was also no significant difference between treatments in mean biomass of mosquitofish

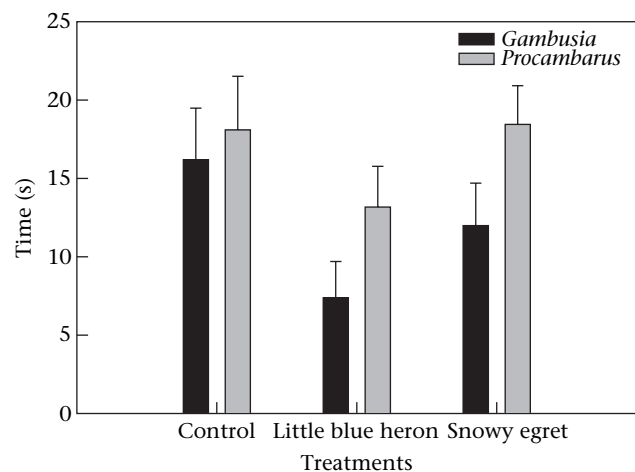


Figure 2. Time spent in front of treatment during 1-min observation by two prey species: *Gambusia* (open water control: $N = 37$; dark: $N = 37$; white: $N = 37$) and *Procamburus* (control: $N = 34$; dark: $N = 41$; white: $N = 45$). Control = dowel; dark = little blue heron model; white = snowy egret model.

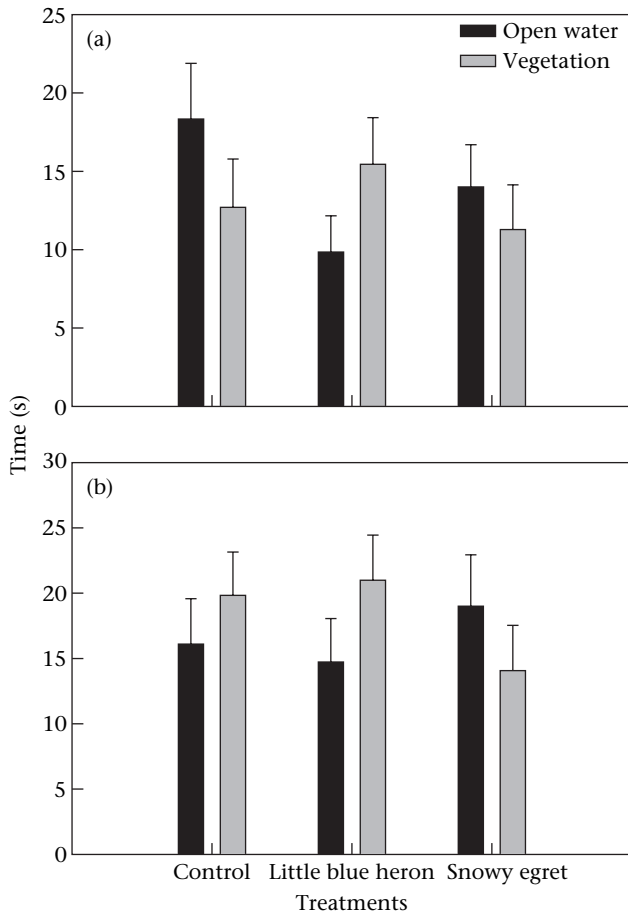


Figure 3. Time spent in front of treatment during 1-min observation for (a) *Gambusia* (open water control: $N = 40$; dark: $N = 40$; white: $N = 40$; vegetation control: $N = 40$; dark: $N = 40$; white: $N = 40$) and (b) *Procambarus* (open water control: $N = 30$; dark: $N = 30$; white: $N = 30$; vegetation control: $N = 30$; dark: $N = 30$; white: $N = 30$). Control = dowel; dark = little blue heron model; white = snowy egret model.

captured in open water ($T_2 = 1.08$, $P > 0.20$) or vegetation ($T_2 = 1.317$, $P > 0.20$).

There was also no significant difference between the three treatments in mean biomass of frogs captured in open water ($T_2 = 0.817$, $P > 0.20$) and in vegetation ($T_2 = 0.670$, $P > 0.20$), or in mean biomass of crayfish captured in open water ($T_2 = 0.035$, $P > 0.20$) and in vegetation ($T_2 = 0.075$, $P > 0.20$).

DISCUSSION

Quantification of Spectral Reflectance

White plumage from a snowy egret appears to be more highly reflective than are blue-plumaged feathers from a little blue heron. White plumage was also more reflective than was living or senesced vegetation, indicating the greater potential conspicuousness of white plumage than blue plumage against a vegetative backdrop. The reduced reflectance for blue plumage suggests the potential for greater crypsis of blue plumage against a vegetative

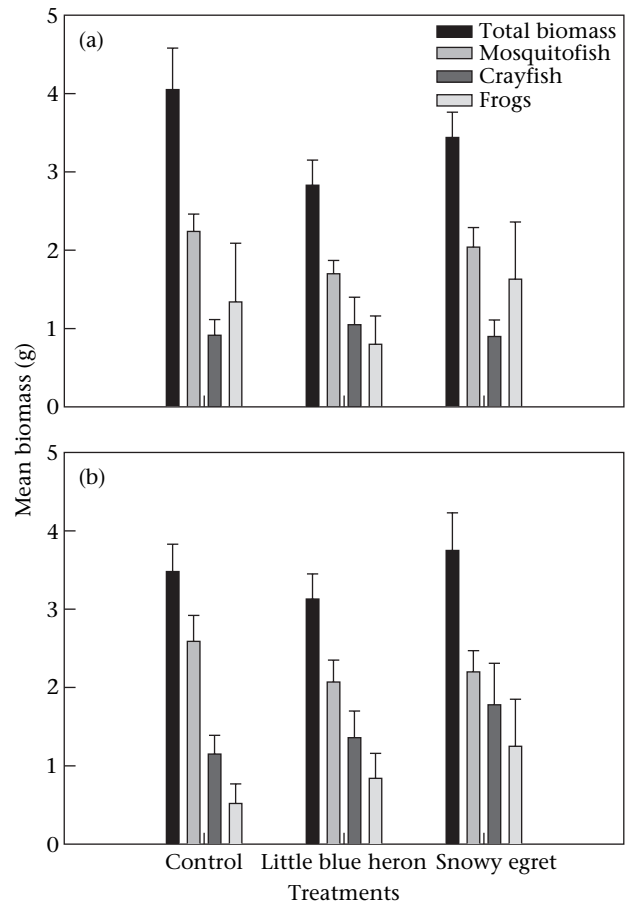


Figure 4. Mean total biomass, *Gambusia* biomass, *Procambarus* biomass, and Hylidae biomass in each treatment for two habitats: (a) open water ($N = 81$) and (b) vegetation ($N = 58$).

backdrop. Our reflectance data suggest that in open water, white plumage may be more cryptic than blue plumage.

Laboratory Studies: Effects of Plumage Colour and Habitat

Both prey species spent approximately one-third of the time in front of the control, suggesting that a 1-min observation period was sufficient time to detect a response. In experiment 1, mosquitofish responded to the treatments by avoiding the little blue heron mount in open water. However in experiment 2, there was no significant response towards either plumage mount in open water, although the tendency to avoid the little blue heron was similar to that in experiment 1. The reasons for the differences in responses between the first and second experiments are unclear. Contrary to our predictions, mosquitofish did not respond to either treatment in vegetation. Mosquitofish showed the ability to detect the little blue heron mount in open water as something to be avoided and responded accordingly. With no backdrop, simulating a bird standing in open water, our results suggest that the little blue heron mount may have been less cryptic than the snowy egret mount. For

mosquitofish, our results support the hypotheses that white plumage is more cryptic and that dark plumage is more conspicuous in open water.

Based on differences in vision, we predicted that crayfish would respond less to plumage colour and habitat. However, crayfish showed no detectable differences in either avoidance of or movement towards plumage colour or a backdrop. The visual abilities of fish and crayfish, two common prey items of herons, vary considerably. The vision of fish is similar to that of terrestrial vertebrates; they have paired, image-forming eyes that can distinguish hue, brightness, texture and contour (Guthrie 1986). Fish have a mediated 'startle response' to moving objects on the surface and subsurface that is presumably controlled by the giant Mauthner cells (Eaton & Bombardieri 1978). Crayfish, like other arthropods, have compound eyes and are mostly limited to short-distance vision (<20 cm; Land 1981). Crayfish have superposition eyes that serve them well in poorly lighted habitats (Ruppert & Barnes 1994). Visual differences between mosquitofish and crayfish presumably influenced the differences in responses that we observed. In the field, dark-plumaged herons (e.g. little blue herons, great blue herons) forage more on crayfish and other crustacean species, but white-plumaged herons (e.g. snowy egret, great egret) forage more on various fish species (Smith 1997; C. Green, unpublished data).

Field Study: Effects of Plumage Colour and Habitat

The total prey biomass that was captured did not differ between treatments. However, within open (unvegetated) water, we captured the fewest prey using the little blue heron mount, and captured the most biomass with the snowy egret mount and control; these differences were not observed in vegetation, where we captured similar amounts of prey between treatments. Our results support the hypothesis that dark-plumaged birds are less cryptic in open water. Contrary to our other hypothesis, white-plumaged birds were not more conspicuous in vegetation, because all three treatments contained similar amounts of prey. Within prey species, we found no significant differences in biomass between treatments or within habitats. Mosquitofish and frogs tended to avoid the little blue heron in open water, although no one prey species significantly avoided a specific treatment.

We hypothesized that white-plumaged birds would be both more cryptic in open water and less cryptic in vegetation than would dark-plumaged birds. Our results from the laboratory and field support the first hypothesis but reject the second hypothesis. Certain prey (mosquitofish and frogs) tended to detect and avoid the presence of a dark object in open water. Although we cannot conclude that these prey species detected the presence of a little blue heron, they did appear to respond to the contrast in colour between a little blue heron and a clear sky and move away from the mount. Our results suggest that in vegetated habitats (e.g. more complex structure), prey may not be able to detect differences in contrasting coloration.

In vegetation, differences in plumage colour between predators may not confer an advantage to one colour when foraging on mosquitofish, crayfish or frogs.

Our experiments all involved stationary study skin mounts, so our results presumably apply only to scenarios involving stationary foraging herons using common foraging tactics such as 'stand and wait', 'peering' and 'foot shuffle/rake' (Kushlan 1978; Green 2003). Herons and egrets spend the majority of their time foraging using such passive or stationary foraging tactics (Rodgers 1983; Green 2003). If plumage colour does influence crypsis to prey in open water, then foraging tactics may differ between dark- and white-plumaged herons under these conditions. White herons, under increased crypsis in open water, may exploit this enhanced crypsis using passive foraging tactics.

In summary, dark-plumaged birds appear to be less cryptic in open (unvegetated) water habitats. In vegetation, we found no differences between prey numbers near little blue herons and snowy egrets, suggesting no adaptive advantage to specific plumage colour in vegetated habitats. Our results indicate that white plumage may confer an ecological advantage for wading birds foraging in open water habitats. Conversely, dark-plumaged birds may be at a disadvantage foraging in open water. The ecological advantage for dark-plumaged herons in relation to foraging behaviour is unclear. Future studies should investigate other selective pressures (e.g. thermal properties, predator avoidance) that may act upon dark plumage colour in herons.

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