

Plumage Dimorphism in the Reddish Egret: Does Plumage Coloration Influence Foraging Habitat Use and Tactics?

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Abstract.—One possible explanation for the evolution of white plumage in herons is an adaptive advantage for foraging. Under this hypothesis, white plumage is cryptic to aquatic prey; thus white-plumaged birds may be more prone to forage in deep water habitats, where they would be cryptic, using passive foraging tactics. Dark-plumaged birds foraging in shallow water habitats, where they are presumably more visible, use active tactics. These hypotheses were tested by investigating choice of water depth and choice of foraging tactics by conducting paired foraging observations between color morphs within the plumage dimorphic Reddish Egret (*Egretta rufescens*). Water was divided into four depths classes: deep (>15 cm), intermediate (5-15 cm), shallow (1-5 cm), and mudflat (<1 cm). There was no difference in time spent in different water depth classes between the two color morphs of the Reddish Egret. However, there was a significant interaction between color morph and depth of water for time spent actively foraging. The white morph of the Reddish Egret was more active in intermediate depths of water than the dark morph while the dark morph was more active in shallow depths of water. These results support the hypothesis that Reddish Egrets may alter foraging tactics based on their degree of crypsis to prey. Received 3 March 2005, accepted 14 July 2005.

Key words.—Reddish egret, *Egretta rufescens*, foraging behavior, plumage coloration, white plumage, herons.

Waterbirds 28(4): 519-524, 2005

Current phylogenies of Ardeidae suggest white plumage has evolved independently on numerous occasions (Sibley and Ahlquist 1990; Sheldon *et al.* 1995). The apparent independent evolution of white plumage in herons has long intrigued biologists, producing several proposed explanations for the widespread occurrence of white plumage in Ardeidae (Mock 1980; Tickell 2003). Across long-legged wading bird species, there seems to be a general dichotomy between dark and white plumage (Kushlan 1978). Furthermore, within the family Ardeidae, six species show two distinct color morphs (Mock 1980). The presumably adaptive significance of plumage coloration in herons has been a subject of debate for some time (Palmer 1909; Mayr 1945, 1956; Huxley 1955; Recher and Recher 1969; Murton 1971; Holyoak 1973; Bolen and Cottam 1975; Caldwell 1986; Tickell 2003). One possible explanation for the evolution of white plumage is an adaptive advantage for foraging under certain conditions (Kushlan 1978; Mock 1980). White plumage has been shown to enhance crypsis to aquatic prey in comparison with dark plumage in Ardeidae (Mock 1980; Green and Leberg 2005).

Investigations of the ecology of the Reef Heron (*Egretta sacra*) initiated discussions of

the influence of plumage polymorphisms on foraging behavior (Murton 1971; Harvey 1975; Rohwer 1990). This species has both white and dark plumage morphs. Murton (1971) suggested that the ratio of color morphs was correlated with environmental features of the habitat and he postulated that a particular plumage might be more advantageous (e.g., enhanced crypsis) in a specific habitat. He also suggested that color polymorphism in herons may be a means for increased resource partitioning (Murton 1971). Observing Reef Heron morphs in French Polynesia, Holyoak (1973) noted white-plumaged herons were more common on white (coral) beaches and conspicuously absent on dark (sand) beaches. Rohwer (1990) postulated that differences in habitat use might reflect differences in exploitation of microhabitats based on color morphs. He further stated that these differences in exploitation might influence the foraging efficiencies in specific habitats for each morph.

Kushlan (1978) developed a series of hypotheses on how plumage coloration should influence habitat use, foraging behavior, and sociality. He suggested that social birds should have light dorsal plumage for increased conspicuousness while solitary birds

should have dark dorsal plumage. Additionally, birds foraging mostly in open water should have light ventral plumage while foragers in emergent vegetation or shade should have dark ventral plumage. Using these hypotheses, Kushlan (1978) accurately predicted the dorsal and ventral plumage coloration for 27 of 31 species on the basis of published reports of habitat use and foraging behavior. There have been no field tests of these hypotheses.

Hérons employ numerous foraging tactics (Kushlan 1978). Active behavior often utilized by herons includes "walking quickly", "running", "open-wing" and "aerial" techniques (Rodgers 1974, 1983). Passive foraging behavior is usually "stand and wait", "peering", "foot raking" and "slow walking" (Rodgers 1983). Dimalaxis *et al.* (1997) attributed the use of specific foraging tactics by herons to a specific habitat. The Grey Heron (*Ardea cinerea*), Great Egret (*Ardea alba*), Little Egret (*Egretta garzetta*) were observed using active foraging tactics in shallow, vegetated marshes while birds foraging in deep water habitats used passive foraging tactics.

Murton (1971) suggested that specific color morphs of herons might favor specific foraging tactics. Under the assumption that white plumage increases crypsis, Murton (1971) argued that white birds should use surprise foraging (stand-and-wait method) while dark birds should favor scaring prey (active or pursuit methods). In the Reef Heron, Rohwer (1990) observed dark herons using more active (pursuit) methods. He noted differences between morphs in foraging tactics, citing "flight-freeze" methods employed by white birds on breaking surfs and active walking/running on reef flats by the dark morphs. However, Recher (1972) and Itoh (1991) found no differences in foraging tactics between dark and white morphs of the Reef Heron.

The foraging ecology of white and dark morphs of the Reddish Egret was examined, and results are presented here in terms of habitat use, strike efficiency, capture rates, and foraging tactic use. Based on their degree of crypsis to prey (Green and Leberg 2005), white and dark morphs should differ

in their foraging tactics and depth of water use. Both morphs of the Reddish Egret commonly forage on non-vegetated tidal flats (Farmer 1991). Thus, I predicted that white morphs should utilize deeper water (>15 cm) foraging habitats in relation to dark morphs. White and dark morphs should also utilize different foraging tactics based on their degree of crypsis. I predicted that white morphs would use passive tactics in deeper waters while dark morphs would use active tactics (pursuit) in shallower waters.

METHODS

Study Areas

Both morphs of the Reddish Egret were studied at Laguna Atascosa National Wildlife Refuge (LANWR) near Rio Hondo, Texas during December-January and June-July from 2002-2003. At LANWR, 40%-50% of the birds occurred as the white morph (Steve Labuda, LANWR refuge manager, pers. comm.; Richard Gibbons, Coastal Bend Bay and Estuaries, pers. comm.).

Hypothesis 1: Differences in habitat use and foraging efficiency

Does the white morph of the Reddish Egret spend more time in deeper waters than the dark morph of the Reddish Egret and conversely, does the dark morph spend more time in shallower waters? Birds were typically observed for ≤ 20 min. and the depth of water being utilized was recorded throughout the observation period. Observations were conducted during the day approximately between 10.00 h and 15.00 h to minimize the bird's shadow on the water from low-angle sunlight. All observations were paired; a focal bird was observed from each color morph of the Reddish Egret for the specified period of time. All observations were made using a spotting scope and recorded on a cassette tape-recorder. Both observations for each color morph pair were conducted in the same given area to assure equal depth of water availability to both focal birds.

The foraging behavior of the Reddish Egret was examined in relation to the use of specific depths of water. Because the Reddish Egret at LANWR almost exclusively utilize tidal flats with water depths ≤ 20 cm (Farmer 1991), available habitat was classified as all tidal flats in a given area with depths ≤ 20 cm. The foraging habitat was *a priori* subdivided into four classes: deep (≥ 15 cm), intermediate (5-15 cm), shallow (1-5 cm), and mudflat (≤ 1 cm). The habitat classes were assigned based on how much of the bird's leg was submerged when the bird was standing upright in the water.

Statistical analyses were conducted using paired t-tests, blocked by observation pair (one dark morph and one white morph) to control for environmental variations (PROC TTEST, SAS Institute 1999). The dependent variables were time spent in shallow water, intermediate water or deep water, the three most commonly used water depths. Strike efficiency and capture rate were analyzed within each depth of water class. Poisson regression was used to analyze differences in

strike efficiency and capture rates within each pair between depths of water classes (PROC GENMOD, SAS Institute 1999). The number of strikes or observation time was used as offsets in the models. Because of the dynamic nature of tidal flats, observations were blocked by pair to account for environmental variations within and between observation days. If one or both morphs in an observation pair moved between more than one water depth of class per observation period, only the foraging data for the proportion of time spent in the same depth class by both morphs of an observation pair were analyzed. To avoid pseudoreplication, no more than one depth class per observation pair was used for the foraging analysis. If, within an observation pair, no common depth class was used by both morphs, that pair was dropped from the analysis. The dependent variables in these analyses were either the number of captures/number of strikes (strike efficiency) or the number of captures/min (capture rate).

Hypothesis 2: Differences in foraging tactic use

Do white birds use more passive foraging tactics than dark birds in deep water? The use of foraging tactics was examined using the same observation protocol described above to test differences in habitat use, strike efficiencies, and capture rates. For each focal bird, plumage morph, relative location, depth of water, foraging tactic, strikes, and captures were recorded. During transcription of each taped feeding bout, each individual foraging tactic was rounded off to the next whole second. The standard terminology of foraging tactics was used following Kushlan (1978), and Rodgers (1983). "Slow walk" was defined as locomotion ≤ 1 step per second, "walk" as $>1 \leq 2$ steps per second, and "run" as >2 steps per second. "Open wing" is the extension and occasional flapping of wings when running, while "flight/hover" is flapping of wings when airborne. A split-plot ANOVA was used and blocked by observation pair for the analyses. Only foraging data from the proportion of observation time that both birds (within the focal pair) spent in the same depth class were used. The dependent variable was the proportion of time spent actively foraging (slow walk, walk, run, open wing, flight/hover). Differences in the amount of time using a specific foraging tactic were also analyzed within species pairs.

RESULTS

Hypothesis 1—Differences in habitat use and foraging efficiencies

Forty-two paired observations were conducted for a total of 1,552 min of observation

time. Both color morphs spent similar amounts of time in each depth of water (Table 1). No significant differences in habitat use was found between the two Reddish Egret morphs in Shallow ($t_{41} = 1.55$, n.s.), Intermediate ($t_{41} = 0.81$, n.s.) and Deep waters ($t_{41} = 0.70$, n.s.). Because both color morphs spent less than 1.0% of the time foraging on mudflats, this habitat class was dropped from all analyses for hypothesis 2.

There was no interaction between depth of water and plumage coloration for the strike efficiencies of the two color morphs ($\chi^2_2 = 0.41$, n.s., Table 2). The two color morphs also did not differ in strike efficiencies ($\chi^2_1 = 0.02$, n.s.). There was no significant interaction between depth of water and plumage coloration for the capture rates of the two color morphs ($\chi^2_2 = 0.06$, n.s.). Reddish Egret color morphs did not differ in capture rates ($\chi^2_1 = 0.56$, n.s.) but both color morphs had increasing capture rates as depth of water decreased ($\chi^2_2 = 33.4$, $P < 0.001$).

Hypothesis 2—Differences in foraging tactic use

There was a significant interaction between plumage coloration and depth of water as the two color morphs of the Reddish Egret significantly differed in their amount of time spent actively foraging ($F_{2,32} = 4.68$, $P < 0.02$, Fig. 1). White morphs spent approximately 17 percent more time actively foraging in intermediate depths of water than dark morphs while dark morphs spent approximately 14 percent more time actively foraging in shallow waters. Both morphs spent similar amounts of time actively foraging in >15 cm of water.

The Reddish Egret exhibited a wide range of foraging tactics. The most commonly used foraging tactics were "stand and wait" (passive), "slow walk" (active), "walk" (ac-

Table 1. Intraspecific comparison of mean amount (percent) of time spent in each depth of water for the color morphs of the Reddish Egret (N = 42). Error estimates are standard error.

Morph	Deep	Intermediate	Shallow	Mudflat
Dark	20.1 \pm 5.7	63.7 \pm 6.5	15.3 \pm 4.6	0.4 \pm 0.3
White	17.4 \pm 5.6	58.4 \pm 6.7	23.4 \pm 5.5	0.7 \pm 0.5

Table 2. Intraspecific comparison of mean strike efficiency (# of captures/# of strikes) and mean capture rate (#/min) for both color morphs of the Reddish Egret by depth of water class. N refers to the number of observations pairs in each depth class. Error estimates are standard error.

Morph	Strike efficiency			Capture rate		
	Deep (N = 7)	Intermediate (N = 21)	Shallow (N = 7)	Deep (N = 7)	Intermediate (N = 21)	Shallow (N = 7)
Dark	0.50 ± 0.08	0.41 ± 0.06	0.45 ± 0.05	0.25 ± 0.04	0.62 ± 0.12	1.72 ± 0.22
White	0.45 ± 0.11	0.44 ± 0.05	0.32 ± 0.07	0.28 ± 0.06	0.89 ± 0.13	1.83 ± 0.53

tive), and “run” (active). There was a significant interaction between depth of water and color morph for time spent using “stand and wait” tactic ($F_{2,32} = 4.66$, $P < 0.02$, Fig. 2). White morphs used “stand and wait” approximately 16% more often in shallow waters (<5 cm) while dark morphs used “stand and wait” approximately 12% more often in intermediate waters (5-15 cm). There was no significant interaction between depth classes and color morphs in time spent using “slow walk” ($F_{2,32} = 1.94$, n.s.). There was a significant interaction between depth of water and color morph in time spent using a “walk” tactic ($F_{2,32} = 3.60$, $P < 0.04$). In intermediate depths of water, white morphs used “walk” tactic approximately 7% more often than dark morphs while in shallow waters, dark morphs used “walk” tactic approximately 9% more often than white morphs. There was

no significant interaction in the time spent using “run” for color morphs by habitat ($F_{2,32} = 2.64$, n.s.). Both morphs spent more time using “run” tactic in intermediate and shallow waters than in deep waters ($F_{2,32} = 14.9$, $P < 0.001$).

DISCUSSION

Hypothesis 1—Differences in habitat use and foraging efficiencies

Based on differential degrees of crypsis to prey, white morphs of the Reddish Egret pair were *a priori* predicted to use deeper waters to forage passively while dark morphs were predicted to use shallower waters to actively pursue prey. For both color morphs, there was no difference in time spent in each depth of water class. Strike efficiencies and capture rates did not differ between color morphs or between habitats. In retrospect, it is perhaps not surprising that the observed strike efficiencies and capture rates between morphs were similar because an individual should forage in areas and use specific tactics that promote efficiency.

Hypothesis 2—Differences in foraging tactic use

Based on conspicuousness to prey, white morphs were *a priori* predicted to be more passive foragers than dark morphs. Both color morphs utilized a wide range of foraging tactics with both nearly identical in proportion of time spent using each foraging behavior without regard to depth of water. These results are in accordance with earlier studies of Reddish Egret foraging behavior that also did not include water depth (Rodgers 1983). However, when water depth was included in

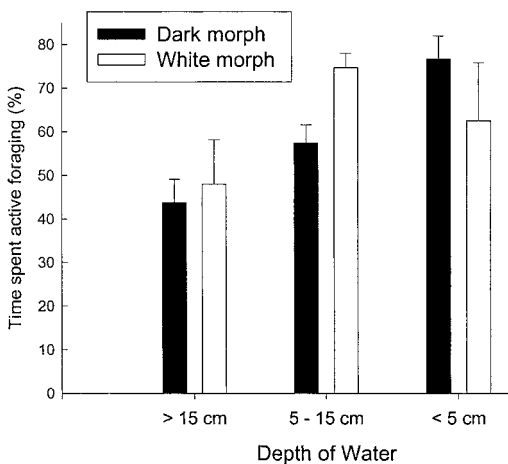


Figure 1. Comparisons of the percentage of time spent active foraging by the Reddish Egret within each depth of water: (dark) > 15 cm: N = 7, 5-15 cm: N = 21, <5 cm: N = 7; (white) >15 cm: N = 7, 5-15 cm: N = 21, <5 cm: N = 7). Error bars represent standard error.

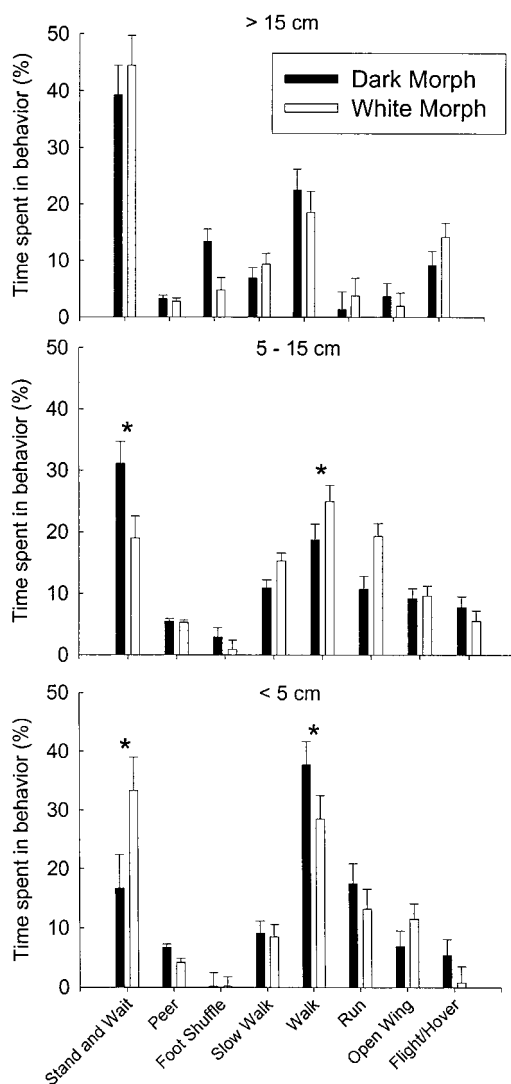


Figure 2. Comparison of the amount of time (percentage) spent using specific foraging tactics by the Reddish Egret morphs compared across depth of water classes: (dark) >15 cm: N = 7, 5-15 cm: N = 21, <5 cm: N = 7; (white) >15 cm: N = 7, 5-15 cm: N = 21, <5 cm: N = 7. Error bars represent standard error. An “*” indicates a significant interaction ($\alpha = 0.05$) between depth of water and color morph for time spent using the specified foraging tactic.

the analysis, differences in time spent actively foraging by habitat were significant between the two color morphs. These proportions varied as white morphs spent more time actively foraging (“walk”) in intermediate water depths while dark morphs spent more time actively foraging (“walk” and “run”) in shallow waters. In deep water, both

morphs exhibited reduced times actively foraging, using “stand and wait” as the predominant passive tactic. These differences have not been previously reported. In deep waters (>15 cm), both morphs use of active tactics are presumably constrained by depth of water and would predictably be less active foragers. At these depths, water is above the tarsus-metatarsus joint and approaches the body of the bird “wades” through the water. In depths of less than 15 cm, birds are presumably less restricted in their use of tactics and should employ tactics that yield the highest foraging efficiency.

Passive foraging in open waters and more active foraging in shallower waters by Reddish Egrets suggest possible influence of plumage coloration on foraging tactics (Murton 1971; Rohwer 1990). The evolution of white plumage in herons has often been attributed to foraging behavior of herons and an increase in crypsis to aquatic prey (Kushlan 1978; Mock 1980; Green and Leberg 2005). Evidence for this hypothesis in other waterbirds is supported by both observational and experimental studies (Craik 1944; Cowan 1972; Gotmark 1987). While it is difficult to determine the selection pressures that may have resulted in the evolution of white plumage, our results suggest possible current adaptive advantages to foraging.

While the evolution of white plumage has generated much discussion and research, the adaptive advantages of dark plumage has generated considerably less attention (Recher, 1972; Mock, 1980). Under the assumption of differential crypsis to prey, white morphs should be more passive in deep waters while dark morphs should be more active in shallow waters. Both morphs spent similar amounts of time actively foraging in deep water; however in support of the predictions, dark morphs spent more time actively foraging in shallow waters. Observations of the Reddish Egret provide evidence that dark-plumaged birds employ active tactics to pursue prey. In accordance with the tested hypotheses, the increase in active foraging over the white morph is greatest in the shallow water, suggesting that the dark morph is less

cryptic. These results support the hypothesis that plumage coloration may influence foraging tactics and specifically that the Reddish Egret may alter its foraging behavior based on their degree of crypsis to prey.

ACKNOWLEDGMENTS

I thank P. Leberg for his guidance and suggestions on my research and constructive comments for this manuscript. J. Coulson provided valuable comments on an earlier draft of this manuscript. I thank L. Laack and M. Fernandez for assistance and housing while conducting observations at Laguna Atascosa National Wildlife Refuge. C. Jeske and the USGS National Wetlands Research Center were instrumental in providing logistical support. This research was supported in part by The University of Louisiana at Lafayette Graduate Student Organization Supply Fund, Sigma Xi Grants in Aid of Research, and Waterbird Society Grant in Ciconiiform Biology and Conservation.

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