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Author(s): Zachary Holderby, William Simper, Brock Geary and M. Clay Green

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Potential Factors Affecting Nest Initiation Date, Clutch Size and Nest Success in the Plumage Dimorphic Reddish Egret

ZACHARY HOLDERBY¹, WILLIAM SIMPER², BROCK GEARY² AND M. CLAY GREEN^{1,2,*}

¹Department of Biology, Wildlife Ecology Program, Texas State University-San Marcos, San Marcos, TX, 78666, USA

²Department of Biology, Population and Conservation Program, Texas State University-San Marcos, San Marcos, TX, 78666, USA

*Corresponding author, Internet: claygreen@txstate.edu

Abstract.—Plumage dimorphism is common in the family Ardeidae with one morph possessing all-white plumage and the alternate morph being darkly colored. The effects of plumage morph and colony site on nest initiation date, clutch size and total nest success of the plumage dimorphic Reddish Egret in the Laguna Madre region of Texas were examined. Color morph did not significantly affect nest initiation date (Julian date - Dark morph: 109.88 (S.D. 26.56), White morph: 100.82 (25.85), Mixed-morph: 113.29 (27.55); ANOVA: $F_{(2,158)} = 0.199$, $P = 0.820$) although nest initiation date was different between nesting colonies (Julian date - Rabbit Island: 125.14 (S.D. 18.05); Zigzag Island: 87.15 (19.07); ANOVA: $F_{(1,158)} = 5.732$, $P = 0.018$). Overall mean (\pm S.E.) clutch size was 3.29 ± 0.05 and differed between colony sites but not between color morphs. Model selection analysis using logistic exposure revealed that neither plumage morph nor colony site had a significant effect on nest success. Mayfield total nest success was estimated at $85.10\% \pm 5.4\%$ ($n = 171$), results which are similar to nesting success estimates in other heron species. The lack of effect of color morph on timing of nest initiation, clutch size and nest success suggests other factors may influence the maintenance of color dimorphism in Reddish Egrets. Received 21 October 2011, accepted 7 March 2012.

Key words.—*Egretta rufescens*, logistic exposure, nest initiation, nest success, polymorphism, Reddish Egret.

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The study of plumage dimorphism is a topic of great interest in avian biology, particularly in waterbirds (Galeotti *et al.* 2003; Roulin 2004). In the case of species where dimorphism is genetically maintained, several hypotheses have been developed to explain the ecological significance of plumage dimorphism. Among these hypotheses are detectability and predator avoidance (Mock 1980; Galeotti *et al.* 2003; Green and Leberg 2005a), congregation and mating preferences (Roulin 2004; Green and Leberg 2005b; Green and Leberg 2006), feeding ecology (Mock 1980; Roulin 2004; Green 2005), and the occurrence of white plumage as a default in the absence of phenotypic costs (Tickell 2003). The occurrence of plumage dimorphism allows the possibility of sympatric divergence of a dimorphic species through resource partitioning or reproductive isolation. Recent studies have attempted to expose the mechanisms that maintain or segregate morphs (Smith and Skulason 1996; Galeotti *et al.* 2003; Munday *et al.* 2003; Roulin 2004; Gray and McKinnon 2006). The amount of gene flow among sympatric

morphs changes both temporally and spatially, and if restricted can lead to the divergence of species (Smith and Skulason 1996). Gene flow restriction could occur because of pre-zygotic barriers such as timing of reproduction, or post-zygotic barriers such as reduced fitness of hybrids. Differences in timing of nesting between different morphs could lead to temporal reproductive isolation (Smith and Skulason 1996). Asynchronous nesting between color morphs would presumably result in fewer opportunities to breed with members of the opposing morph. These kinds of isolating mechanisms may co-evolve with polymorphism and ecological adaptations (Smith and Skulason 1996) such as foraging strategy. Traits important in reproductively isolating populations can be correlated to the traits important in utilizing resources (Smith and Skulason 1996). For instance, if plumage is used in mate choice it would isolate dark-plumaged morphs from white-plumaged morphs, and could restrict gene flow between the two morphs. In addition, plumage is important when utilizing resources since plumage provides camou-

flage during foraging (Caldwell 1986; Green and Leberg 2005a) and could affect an individual bird's foraging success and fitness.

Differences in clutch size and nest success between color morphs co-occurring in the same colony may reflect environmental effects on nesting and foraging ecology during the breeding season. In a review on color polymorphism in birds, plumage polymorphism was correlated with at least one reproductive parameter in 14 of 16 (88%) species studied; plumage polymorphism was correlated with clutch size in one species and with nesting success in four species (Roulin 2004). The influence of plumage coloration on crypsis to prey (Green 2005; Green and Leberg 2005a) could potentially affect clutch size and nest success through enhanced or diminished ability for parents to provide nourishment for young in the nest. Studies of clutch size and nesting success between sympatric color morphs may reveal the fitness consequences of an individual's particular plumage color.

The Reddish Egret (*Egretta rufescens*) is a threatened, plumage-dimorphic heron that occurs throughout coastal North and Central America (Lowther and Paul 2002). The ratio of dark morph to white morph Reddish Egrets in populations decreases from west to east, within the species' range; populations in the Pacific coast are made up of entirely dark morphs (Howell and Pyle 1997), the Texas area populations are composed of ~65 percent dark individuals (Amy Hanna, TPWD, unpubl. data), and the easternmost populations in the southern Bahamas are about 85% white (Bolen and Cottam 1975; Green *et al.* 2011). Local adaptation to environmental conditions that favor one morph could potentially contribute to the differences in these ratios; the favored morph would enjoy higher fitness, leading to individuals of that morph predominating in the population (Antoniazza *et al.* 2010).

Our study was part of a larger investigation of the reproductive and foraging ecology of the Reddish Egret and designed to elucidate the underlying mechanisms that maintain the occurrence of color morphs. Differences have been detected in foraging strategies be-

tween Reddish Egret morphs in Texas (Green 2005), but the effects of these strategies on nest initiation and the care of young (leading to effects on reproductive success) have not been measured. The objectives of our research were to examine potential differences in nest initiation date, clutch size and nest success between the two color morphs and any effects of colony site location. We conducted this survey in Texas where both color morphs occur, although dark morphs appear to be the dominant color morph.

METHODS

The study was conducted on two dredge-spoil islands, Rabbit Island (RI, 27° 14' 56" N, 097° 24' 50" W) and Zigzag Island (ZI, 27° 37' 58" N, 097° 16' 01" W), in the hypersaline Laguna Madre of the Texas coast during March-July 2007. Nest surveys were conducted as part of another study investigating use of flight-line counts to survey Reddish Egret colonies (Simper *et al.*, unpubl. data.). Color morph of nests (dark, white or mixed-morph) was determined by visual observation of hatched young and/or parents at the nest. We did not observe both parents at every nest but used the cues of nest attendance by parents in addition to plumage color of hatchlings to assign each nest a color morph type. Mixed-morph nest was defined as a nest with both white and dark morph hatchlings. Reddish Egrets nest in low vegetation within mixed-species waterbird colonies on coastal islands in Texas (Lowther and Paul 2002). Nest initiation date was defined as the date (Julian) the first egg was laid in a nest; this was determined through a series of weekly nest checks. During these searches, nests that were empty, with eggs, or with chicks were recorded. Reddish Egrets typically lay 3-4 eggs in a clutch (Bent 1926) and incubate eggs approximately 29-30 days (McMurry 1971). Hatch date was estimated by chick size for nests that had eggs and then hatched between consecutive nest checks; we selected the midpoint dates between consecutive nest checks to estimate hatch date. If unhatched eggs were in the nest and chicks were less than a week old, then the nest was considered in the hatching stage. Eggs were assumed to be laid every other day (McMurry 1971) therefore chicks were also assumed to hatch approximately every other day. Nests were then categorized as incubating, hatching, brooding or fledgling for each day of the nesting season. Brooding was considered to occur during the first two weeks after hatching. During this period, parents were observed constantly at nests and chicks were relatively stationary. This is consistent with other estimates of egret chick independence (Pratt 1970; St. Clair Raye and Burger 1979; Rodgers 1983). After two weeks, egret chicks explore steadily further from the nest, but do not actually abandon the nest area until they are at least six weeks of age; this period after brooding was categorized as fledgling.

For determining potential differences in nesting initiation date and clutch size between color morphs and colony sites, data analyses were performed using R version 2.5.1© (R Development Core Team 2008). Differences between colony site and color morph in nest initiation dates and clutch size were compared using Type III ANOVA (Zar 1996). For our nest success analysis, we utilized the recently developed, more robust logistic exposure method (Shaffer 2004) to perform model selection and assess the effects of island and morph on nest success, along with the classic Mayfield method (Mayfield 1961) to estimate total nest success rates. Presence or absence of differences in initial nest success between the Reddish Egret and these less threatened species could provide some indication of the life stage during which the Reddish Egret suffers the greatest mortality.

Logistic exposure estimates were calculated using PROC GENMOD (SAS version 9.1, SAS Institute, Cary, NC). Color morph and island were used as explanatory variables for each nest in the analyses. We assumed that nest fates were independent from one another and that nests with equivalent values of covariates also had equivalent daily survival probabilities, as is standard in logistic exposure analysis (Shaffer 2004). Because neither color morph experienced colony failure during the study, the assumption of independence of nest fate appears valid. Akaike weights for model selection were derived from Akaike information criteria, adjusted for small sample size (AIC_c).

For Mayfield analysis, we estimated nest success, fledging success, and total nest success. Nest success was defined as period between nest initiation date (or date the nest was first located) and hatch date. Nest success was considered a success if one egg was observed to have hatched. Incubation period length was set at 29.5 days as reported by McMurtry (1971). Many nests did not have sufficient evidence to definitively declare fledging success, so we created a cutoff based on Lowther and Paul's (2002) observation that parents continuously attend young nestlings for about three weeks. For this study, nests were assumed to have been successful if observations of live nestlings were reported for 21 days or more after the first hatch. Similar estimations of fledging success exist in the literature (Frederick and Collopy 1989; Frederick *et al.* 1992). If insufficient observations (< 21 days after hatch) existed, the nest was considered unreliable for measuring fledging success and removed from the dataset. Total nest success values were calculated by multiplying nest success by fledging success (Mayfield 1961).

RESULTS

We documented a total of 194 nests (RI: $n = 95$ nests, 63 dark, 28 white, 4 mixed-morph; ZI: $n = 99$ nests, 51 dark, 45 white, 3 mixed-morph). We found no significant difference in nest initiation date between color morphs (ANOVA: $F_{(2,158)} = 0.199$, $P = 0.820$, Table 1).

Table 1. Mean Julian date for nest initiation date ($n = 194$) of Reddish Egrets by color morph and nesting island in Texas, USA during March-July 2007.

	Colony - Morph	Mean	S. D.
Total	Dark	109.88	26.56
	White	100.82	25.85
	Mixed	113.29	27.55
Total	Rabbit Island	125.14	18.05
	Zigzag Island	87.15	19.07
Rabbit Island	Dark	125.81	19.07
	White	123.34	15.07
	Mixed	128.00	25.63
Zigzag Island	Dark	87.66	18.28
	White	86.18	20.25
	Mixed	93.67	16.77

There was a significant difference in nest initiation date between the two sites (ANOVA: $F_{(1,158)} = 5.732$, $P = 0.018$) while there was no significant interaction between site and color morph (ANOVA: $F_{(2,158)} = 0.047$, $P = 0.955$). Mean (\pm S.E.) clutch size was 3.29 ± 0.05 for all nests. We found no significant difference in mean clutch size between color morphs (Dark 3.32 ± 0.06 , White 3.25 ± 0.07 , Mixed-morph 3.43 ± 0.20 ; ANOVA: $F_{(2,157)} = 0.191$, $P = 0.826$) but did find a significant effect of island on clutch size (Rabbit 3.48 ± 0.07 , Zigzag 3.10 ± 0.05 ; ANOVA: $F_{(1,157)} = 4.172$, $P = 0.043$). There was no significant interaction between color morph and island on clutch size (ANOVA: $F_{(2,157)} = 0.176$, $P = 0.839$).

For estimates of hatching and fledging success, we used a total of 171 and 99 nests respectively. AIC values for logistic exposure analysis favored the null model ($w = 0.496$), which was at least 1.7 times more likely to fit the data than all other models (Table 2). Total nest success ($\pm 95\%$ C.I.) for all morphs and both islands was estimated at $85.10\% \pm 5.4\%$ ($n = 171$). Total nest success for dark morphs, white morphs and mixed morphs were estimated at $84.18\% \pm$

Table 2. Akaike Information Criterion (AIC) from logistic exposure analysis for Reddish Egret nest success in Texas, USA during March-July 2007.

Model	AIC _c	K	Akaike weight
Intercept	89.5125	1	0.496
Island	90.5879	2	0.290
Morph	92.1413	3	0.133
Island+Morph	93.1236	3	0.081

7.2% ($n = 103$), $84.64\% \pm 9.2\%$ ($n = 61$), and $100\% \pm 22.7\%$ ($n = 7$) respectively. Success of Rabbit and Zigzag Islands were $91.10\% \pm 8.5\%$ ($n = 89$) and $79.63\% \pm 8.9\%$ ($n = 82$), respectively. Nest success (incubation period) and fledging success (first 21 days post hatch) were similar and no difference in total nest success, nest success or fledging success was found between color morphs or colony sites (Table 3).

DISCUSSION

Our study is the first to examine the effects of color morph on nest initiation date, clutch size and nest success in Reddish Egrets, as well as the first to estimate nest success in the species. While Reddish Egrets seem to have paired assortatively, the sorting process did not affect nest initiation date. No differences were detected in the initiation date between morphs nesting within the same colony. Further, clutch size was not influenced by color morph.

Reddish Egrets nesting on different islands throughout the Laguna Madre differed in nest initiation dates (~35 days between mean initiation dates). The significant difference in nest initiation date between the two islands may be due to the fact that late-nesting islands provide inferior nesting habitat and birds move there after colonies with better quality habitat have become saturated. However, in years when early-nesting col-

onies had far fewer nesting egrets, numbers of birds on late-nesting colonies did not decrease accordingly (Texas Coastal Program: Texas colonial waterbird database 2004). Birds may also move to these late-nesting colonies in an attempt to renest after predation at an early-nesting colony. Asynchrony in nest initiation dates between colonies may also be related to water flow in the Laguna Madre and local abundance in Sheepshead Minnow (*Cyprinodon variegatus*) populations. Sheepshead Minnow comprise the bulk of the diet for young Reddish Egrets and the species can become very abundant during the Reddish Egret breeding season (Holderby 2008). Relationships between prey availability and nesting initiation date have not been examined for Reddish Egrets. Our findings of significant differences in clutch size between the two colony sites further suggest a potential relationship between prey abundance and reproductive success.

Model selection results indicated that neither island or color morph significantly impacts nest success. Based on this result, it would appear that color morph has no effect on nest success in the Texas population of Reddish Egrets; both morphs exhibited high nest success. Nests in the Laguna Madre region are typically constructed upon hardy, sharp-leaved plants such as Seaside Oxeye (*Borrchia frutescens*) and cacti (*Opuntia* spp.; Pemberton 1922; Lowther and Paul 2002), making access difficult for potential

Table 3. Nest ($n = 171$) and fledging ($n = 99$) success and 95% confidence intervals for Reddish Egrets in Texas, USA during March - July 2007. Time period for estimating nest success was defined as time interval between dates of first egg laid and hatch date (assumed incubation period of 29.5 days). Time period for estimating fledging success was defined as first 21 days post hatch.

	Colony - Morph	Mean	95% C.I.
Nest Success	Total	92.62	97.47 - 88.00
	Dark	92.95	99.22 - 87.05
	White	91.29	99.99 - 83.32
	Mixed	100.00	N/A
	Rabbit Island	96.89	100.00 - 92.65
	Zigzag Island	87.88	96.88 - 79.69
Fledging Success	Total	91.88	96.69 - 87.30
	Dark	90.58	97.60 - 84.03
	White	92.72	99.99 - 85.87
	Mixed	100.00	N/A
	Rabbit Island	94.02	100.00 - 87.56
	Zigzag Island	90.62	97.14 - 84.51

nest predators such as meso-carnivores. Recent human efforts to control predators such as coyotes (*Canis latrans*) and feral hogs (*Sus scrofa*) on the breeding islands in Texas have reduced nest failures of colonial waterbirds (M. C. Green, personal obs.).

We documented 100% nest success rate for mixed morph nests. While complete success was reported, it is difficult to draw inferences from our results due to the very small sample size. Additionally, it was difficult to assign color morph of each nest prior to hatching, so some nests that failed early in incubation stage could have been mixed-morph nests. Mixed-morph pairing and subsequent nesting potentially result in some advantage that is reflected in increased nest success although selection against hybrids is more prevalent (Gray and McKinnon 2006). A future study with increased sample size of mixed-morph nests is needed to test whether mixed-morph pairings have increased nesting success or exhibit similar rates to same-morph nesting pairs.

Though this study did not detect differences in nest initiation date, clutch size or nest success between color morphs, it is a first step in analyzing reproductive parameters of the dimorphic Reddish Egrets. Typically, Reddish Egrets do not reach sexual maturity until 3-4 years (Lowther and Paul 2002). The post-fledging life stage could introduce novel struggles in the life of an individual bird, such as new predators or competitive challenges, and differentially affect juvenile survival between color morphs. Further studies should analyze reproductive parameters across the species' range and aim to identify risks associated with all periods of life, creating a more complete overview of the Reddish Egret's ecology and potential life history differences between avian color morphs.

Initially, high nesting success seems contradictory to the Reddish Egret's threatened status. Reddish Egret populations remain below historical levels and recent trends suggest regional populations are stable or decreasing (Lowther and Paul 2002). Reddish Egret nesting success rate is equal to or higher than recorded rates of much more common waterbirds (Frederick and Collopy

1989; Telfair II and Bister 2004; Samraoui *et al.* 2007). However, Reddish Egret nest failure is most commonly caused by failure of the entire breeding colony (Lowther and Paul 2002). Due to poor breeding conditions, such as lack of rainfall or disturbance, breeding adults may forego nesting (Parnell *et al.* 1988). Even when conditions initially appear suitable and birds begin egg-laying and incubation, colonies are vulnerable to natural disasters such as hurricanes or human-caused disturbances (Parnell *et al.* 1988). We recommend continued protection and management of existing Reddish Egret colonies and encourage investigations into other stages within this species' life history, besides nesting stage, that are presumably having greater effects on Reddish Egret mortality.

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