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INFLUENCE OF AGE AND DISPERSAL ON REPRODUCTIVE SUCCESS OF CLIFF SWALLOWS (*PETROCHELIDON PYRRHONATA*)

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Abstract.–We examined age-related reproductive success and the short-term consequences of dispersal by known-aged Cliff Swallows (*Petrochelidon pyrrhonota*) breeding in Texas from 1975-86. Clutch size increased with age in females, and males and females ≥2 yrs old fledged more young than yearlings. Sixteen percent (76/463) of birds dispersed between breeding seasons and we observed female-biased dispersal. Birds that dispersed to a different colony at age 2 produced 0.91 fewer fledglings post-dispersal compared to the previous year, and birds that dispersed at age 3 produced 0.34 more fledglings post-dispersal compared to the previous year; females experienced greater benefits than males when they dispersed at age 3 yrs. Younger dispersers incur short-term costs which might have important consequences for lifetime reproductive success for a short-lived passerine. However, potential population-level consequences from dispersal costs is likely minimal given the low rate of dispersal we observed.

Keywords: age-dependent, Cliff Swallow, colonial, dispersal, *Petrochelidon pyrrhonata*, reproductive success

Dispersal is widely acknowledged as an important aspect of avian life history due to its effects on population dynamics, gene flow, and the distribution of species (Johnson & Gaines 1990). Dispersal is also a critical behavioral mechanism that allows individuals an opportunity to make adaptive habitat choices when selecting a new breeding location (Chalfoun & Schmidt 2012). Individual success in year *t* (year of breeding pre-dispersal) can result in site-fidelity following success (Brown & Brown 1996; Murphy 1996; Haas 1998; Hazlitt & Butler 2001), or dispersal post-failure (Pärt & Gustafsson 1989; Whittam & Leonard 1999; Piper et al. 2008; Chalfoun & Martin 2010). However, the tendency for birds to relocate after reproductive

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failure is just that, and variation exists in whether a bird disperses after experiencing low reproductive success. This variation likely exists because there are costs and benefits associated with both site fidelity and dispersal (Newton 2008). Thus, understanding the context under which individuals disperse and the associated outcome of that decision will aid in understanding adaptive habitat selection in birds.

Previous evaluations of breeding outcomes after dispersal have reported inconsistent patterns in reproductive success. In some cases, reproductive output was improved after dispersal (Drilling & Thompson 1988; Calabuig et al. 2008; Valcu & Kempenaers 2008), but variation in outcomes post-dispersal may be affected by an individual's sex (Forero et al. 1999; Ward & Weatherhead 2005), whether dispersal was facilitated by the death of or divorce from a mate (Gutiérrez et al. 2011), or dispersal distance (Cline et al. 2013). However, several others have reported no clear benefits to reproductive success after dispersal (Payne & Payne 1993; Robinson & Oring 1997; Shutler & Clark 2003). Changes in reproductive output can be influenced by many other factors in addition to dispersal decisions, and accounting for potential interactions with these other factors may help explain variation in reproductive outcomes after dispersal.

Reproductive success in birds generally increases with age, can be dependent on sex, and in long-lived species sometimes exhibits senescent declines (Lambrechts & Dhondt 1986; Wiktander et al. 2001; Lecomte et al. 2010). Hypotheses that attempt to explain age-related changes in reproduction include age-related improvements of competence and the progressive appearance or disappearance of phenotypes (Forslund & Pärt 1995; Sergio et al. 2014). Because age influences reproductive strategies and can affect settlement decisions (DiQuinzio et al. 2001), age may interact with dispersal to affect whether individuals experience a cost or benefit of dispersal. Understanding patterns in age-related reproductive success is therefore important in understanding the outcome of breeding dispersal.

Given conflicting evidence reported for birds regarding the effect of breeding dispersal on breeding success post-settlement, we aimed to evaluate age-related reproductive success and the short-term consequences of dispersal by known-aged Cliff Swallows (*Petrochelidon pyrrhonota*). We hoped to inform how often and under what contexts dispersal occurs, and whether dispersal is adaptive from the standpoint of improved reproductive success. Based on patterns reported in the literature, we predicted that 1) reproductive success will increase with age and will not differ between sexes, and 2) short-term costs of dispersal (i.e., those incurred the year following dispersal) will be more pronounced in younger individuals. Despite increasing understanding of bird dispersal patterns, basic information on dispersal rates is lacking for many species throughout their range. The Nebraska population has been the focus of most Cliff Swallow studies (Brown & Brown 1996), and here we provide new information about reproductive success and breeding dispersal for this species from a different part of its range. This basic life history information is critical to defining “local” populations, understanding population dynamics, and making informed decisions regarding species conservation and their habitats.

MATERIALS & METHODS

As a colonial passerine, Cliff Swallows nest under bridges and culverts throughout the central and western U.S. (Brown et al. 2017a) and have expanded their range east in recent decades due to the construction of these structures (Brown & Brown 1996). Cliff Swallows are aerial insectivores that forage in groups and exploit patchy, ephemeral food resources near the nesting area (Brown & Brown 1996). Individuals begin reproducing at one year of age, are typically single-brooded, and most often have a four-egg clutch. We used data from a long-term Cliff Swallow banding study from 1975-

86 at four separate colonies near Lake Somerville in Burleson and Washington Counties in east-central Texas (30º20´N, 96º32´W). Distances among all four colonies ranged from 0.7 − 2.6 km and were defined similarly to Brown et al. (2017b) as "birds from groups of nests that interacted at least occasionally in defense against predators or by sharing information on the whereabouts of food" and occupied a shared structure in a given year. Like Brown et al. (2017b), we consider each culvert a colony because they comprise discrete nesting areas and there were no other areas used for nesting between culverts; our study colonies were the only known nesting colonies in the area. Colonies were similar in size and consisted of approximately 100-150 nests each (Sikes & Arnold 1984). The habitat surrounding each culvert was predominantly post-oak savanna interspersed with agriculture and pasturelands.

Methods for banding and nest monitoring are described fully in Sikes & Arnold (1984) and are summarized here. In order to capture the breeding pair on the nest, nests were plugged with cotton before daylight. Cotton and adult birds were subsequently removed and we banded individuals with a silver U.S. Fish and Wildlife Service band, or previously banded birds had band numbers recorded. We numbered nests and monitored them every 4-7 days until young reached 10 days of age, at which time nestlings were banded. We made an effort to mark all birds in a colony. We collected information on clutch size and number of fledglings per nest and reproductive metrics are detailed in Kosciuch et al. (2001).

In this study we examined the influence of age and dispersal on clutch size and number of young fledged for data available from 1975-86. Data from all years were used to analyze the effects of age on reproductive success, and analyses included birds paired with a mate of unknown age. A subset of data from 1982-85 was used for analysis of known-aged pairs and dispersal. For analysis of these parameters, we used two age classes: yearling (birds fledged the previous year), and older (birds 2 yrs or older). Like Wiktander et al. (2001), we recognized the inherent pseudoreplication that occurs with repeated counting of individuals that lived beyond the second year in the older age class. However, our dataset is not a cohort study and thus not a complete re-sampling of the same individuals in every year.

To address the potential effect that colonial breeding might have on individual reproductive success from year to year, we calculated annual and individual reproductive success. Annual reproductive success (ARS) is the mean number of fledglings/pair and is calculated per colony each year. Colonies in our study ranged in ARS within and between years of the study from 0.5 – 3.5 fledglings/pair (see Kosciuch et al. 2001 for additional details). Individual reproductive success (IRS) is the number of fledglings/individual/yr. For example, if a pair fledged three young, the IRS of the male and female was three. We examined pre- and post- dispersal IRS to determine how dispersal influenced IRS. Thus, individual success can increase, decrease or remain the same post-dispersal. We also examined the influence of current year ARS on IRS to assess the relative importance of colony-level success on determining post-dispersal IRS.

We conducted statistical analyses using SAS (SAS Institute 1995) and Program R (R Core Team 2017) and used a significance level of $\alpha = 0.05$. We used chi-square tests of independence to evaluate whether older females had larger clutches more frequently than younger females, and to evaluate whether either sex dispersed more frequently than expected by chance. We used general linear models (PROC GLM; SAS Institute 1995) with clutch size and fledglings/pair as response variables and tested for an effect of age on these metrics of reproductive success using known-age combinations (yearling birds, M1 F1; yearling male and older female, M1 F2+; older male and yearling female, M2+ F1; and older birds, M2+ F2+). To increase sample size and to determine if patterns observed in the known-aged pairs persisted when birds of unknown age were included, we used all data (1975-86), including birds paired with mates of unknown age to test for an effect of age on reproductive success (*sensu* Brown & Brown 1996).

To examine the short-term fitness consequences of dispersal, we refer to the year of breeding pre-dispersal as year *t*, and the year of breeding post-dispersal as year $t + 1$, and calculated the difference in IRS between year *t* and year $t + 1$. An increase in IRS post-dispersal would be a positive difference (benefit) and a decrease in IRS post-dispersal would be a negative difference (cost). By taking the difference between years, we removed the necessity to account for repeated measures on the same individuals. There were five individuals for which we had three successive years of IRS data; for these individuals we excluded data from the first year to account for observations that were not independent, and only included data on the difference in reproductive success between age 2 and 3 yrs. We used difference in IRS between year *t* and year $t + 1$ as a response variable in a general linear model and tested for age and sex effects. We used a Spearman rank correlation to test for a relationship between ARS in year $t + 1$ and IRS $t + 1$, and between IRS in year *t* and IRS in year $t + 1$. We provide results as mean ± *SE*.

RESULTS

Using data from birds paired with a mate of unknown age, we did not find an effect of age on clutch size for males ($f_{1,173} = 0.01$, $P = 0.98$), but did find an effect for females ($f_{1,203} = 11.88$, $P < 0.005$); mean clutch size increased from age 1-4 yrs for females ($\beta = 0.24$). Older females had larger clutches (> 4 eggs) more frequently than yearling females ($\chi^2 = 30.6$, $P < 0.001$, $df = 1$). Using data from birds paired with a mate of unknown age, we found an effect of age on number of fledglings for both males ($f_{1,173} = 7.22$, $P < 0.01$) and females ($f_{1,203} = 17.44$, $P < 0.001$) (Table 1). The mean number of fledglings increased from age 1-4 yrs for males ($\beta = 0.35$) and females ($\beta = 0.46$). No significant trend was present for ages 5-10 yrs for birds of either sex due to small sample size ($n = 12$). We investigated the reproductive output of 59 known-aged pairs of Cliff Swallows. Mean clutch size ($f_{3,56} = 1.10$, $P = 0.34$) and number of fledglings ($f_{3,56} = 1.44$, $P = 0.24$) were not influenced by age combination class of the pair (M1 F1, M1 F2+, M2+ F1, M2+ F2+) (Table 1).

Table 1. Productivity of nesting male and female Cliff Swallows (*Petrochelidon pyyrhonota*) by age combinations from four colonies in east-central Texas, 1975-86. *a* represents all females (all age groups pooled) and *b* represents all males (all age groups pooled).

Age			Clutch Size	Fledglings
Male	Female	n	Mean (± *SE*)	Mean (± *SE*)
1	1	34	4.29 (0.17)	2.38 (0.27)
1	2+	4	4.75 (0.25)	2.50 (1.44)
2+	1	6	3.67(0.99)	2.50 (0.67)
2+	2+	15	4.20 (0.29)	3.27 (0.34)
1	a	95	4.07 (0.12)	1.87 (0.18)
2+	a	79	4.08 (0.13)	2.56 (0.18)
b	1	132	3.80 (0.10)	1.82 (0.14)
b	2+	72	4.33 (0.11)	2.77 (0.18)

We identified 463 individuals that were captured $\geq$ 2 consecutive years; 46% were females and 54% were males; 16% (76/463) dispersed between breeding seasons and we observed female-biased dispersal ($\chi^2 = 6.3$, $P < 0.05$, $df = 1$). Only 4% (5/76) of individuals that dispersed between seasons switched colonies for 3 consecutive years. Individual reproductive success of birds in year *t* that maintained site fidelity (mean number of fledglings = 3.77 ± 0.14, $n = 99$) was significantly higher ($t = 3.46$, $df = 134$, $P < 0.001$) than birds that dispersed (mean number of fledglings = 2.88 ± 0.22, $n = 67$). We found no significant interaction of age and sex ($f_{1,63} = 0.23$, $P = 0.50$) or main effect of sex ($f_{1,63} = 0.67$, $P = 0.42$) on difference in IRS between year *t* and year *t* + 1, but found an effect of age at dispersal on IRS in year *t* + 1 ($f_{1,63} = 4.12$, $P = 0.045$). Mean difference in IRS between year *t* and year *t* + 1 was -0.91 fledglings ± 0.45 ($n = 35$) for birds that dispersed at 2 yrs old, and 0.34 fledglings ± 0.40 ($n = 32$) for birds that dispersed at 3 yrs old (Figure 1). However, the pattern of a reproductive benefit for birds age 3 yrs was driven by females, who experienced a greater increase in the number of fledglings produced than males when they dispersed at age 3 yrs (Figure 1). For birds that dispersed, IRS of year *t* was not correlated ($r = 0.10$, $P = 0.44$) with IRS of year *t* + 1. However, IRS of year *t* + 1 was correlated with ARS of the chosen colony ($r = 0.37$, $P = 0.002$).

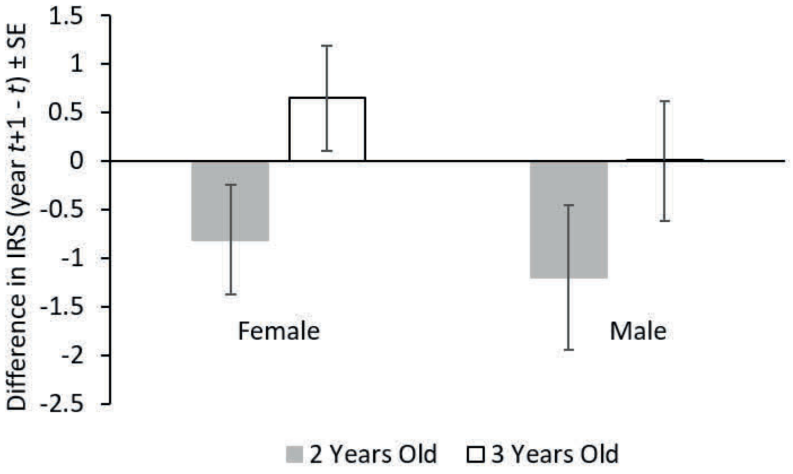

Figure 1. Difference in individual reproductive success (IRS) ± standard error (*SE*) between years *t* and *t* + 1 for Cliff Swallows (*Petrochelidon pyyrhonota*) that dispersed to a new breeding colony at age 2 yrs and age 3 yrs. Data were collected from four colonies in east-central Texas, 1975-86.

DISCUSSION

We found that Cliff Swallows generally (76%) paired with mates of similar age, and that reproductive success increased with age. Brown & Brown (1996) also observed that most pairs of Cliff Swallows are of similar age (80%). Age-assortative mating is documented for other colonial species such as night herons (Fasola et al. 2001), terns (Coulson & Horobin 1976; Nisbet et al. 1984), and gulls (Miller 1973, Coulson & Thomas 1983). Similar patterns of increased clutch size with age have been documented for other non-colonial passerines including Prothonotary Warblers (*Protonotaria citrea*; Blem et al. 1999) and Bluethroats (*Luscinia svecica*; Geslin et al. 2004). Age-related increases in clutch size for female Cliff Swallows, as well as increases in number of fledglings, have been reported from Nebraska (Brown & Brown 1996), but our study represents the first to report age-related patterns from other parts of the species' geographic range (Brown et al. 2017a).

Although fledging success did not differ significantly among known-aged pair combinations, the combination of older males and females fledged approximately 30% more young than all other age combinations, which might represent a biologically important difference. By evaluating patterns of productivity on an individual basis rather than by known-age pair combinations, we observed large increases in number of fledglings with age for both sexes. This pattern translated to increases of nearly 2 fledglings from first year breeders to breeders in their fourth year. Increased fledging success for older males and females is relatively well-documented for passerines (e.g., Holmes et al. 1992, Geslin et al. 2004), and can be influenced by a lack of breeding experience in younger individuals (Forslund & Pärt 1995). Robertson & Rendell (2001) found similar patterns of age-related increased reproductive success for non-colonial, cavity nesting Tree Swallows (*Tachycineta bicolor*).

Estimates of breeding dispersal for Nebraska populations are 40% (Brown & Brown 1996) and for California populations are 20% (Mayhew 1958) and suggest our observed dispersal rates could be underestimated (16% of birds captured ≥ 2 years dispersed to other colonies in our study area); however separating dispersal from mortality in our study is impossible. Like others, we observed female-biased dispersal in Cliff Swallows (Mayhew 1958, Brown et al. 2017b). Females can disperse more readily if they are the limiting sex and, therefore, easily choose males in the new patch (Greenwood 1980). Moreover, if female Cliff Swallows in our study population arrive at breeding colonies later than males, as they do in Nebraska (Brown & Brown 1996), then they may acquire more or different information about breeding prospects than males have access to, which could influence the propensity to disperse among colonies. However, these patterns represent the influence of environmental factors (e.g., landscape and climate) and population dynamics (e.g., colony size and associated parasite loads; Brown et al. 2017b) that have likely changed substantially since these data were collected approximately 40 years ago. Given the role of these variables in potentially influencing dispersal rates and associated consequences for Cliff Swallows, our inference is necessarily restricted in time to the years of our study and values reported here should not be assumed to represent contemporary patterns without further investigation.

Dispersal often occurs after reproductive failure (Brown & Brown 1996), and although not all dispersers failed in year *t*, our results demonstrate IRS was significantly lower in year *t* for birds that dispersed than those that did not. We found short-term costs of dispersal for birds that dispersed at two years of age in the form of decreased mean number of fledglings in year *t* + 1. However, there was an increase in mean number of fledglings for birds that dispersed in year *t* + 1 at three years of age suggesting that older (and presumably, more experienced) birds can overcome short-term costs of dispersal. Moreover, females realized greater reproductive benefits than males when they dispersed at age 3 yrs, suggesting that dispersal is a strategy favoring females in this population and potentially a contributing reason for female-biased dispersal. Dispersal has been demonstrated to carry energetic costs because individuals must find or acquire a new breeding site, are possibly exposed to higher predation risk in the process, and potentially must develop new strategies (e.g., foraging, locating nesting materials) in the new patch (Pärt 1995, Suryan & Irons 2001, Yoder et al. 2004, Kingma et al. 2016). The correlation between IRS in year *t* + 1 and the colony ARS suggests that the local environment of the new breeding colony could be an important factor in determining IRS in year *t* + 1, and thus, the costs or benefits associated with dispersal.

We found increases in reproductive success with age, but younger dispersers incur short-term costs which might have important consequences for lifetime reproductive success for a short-lived passerine. However, potential population-level consequences from dispersal costs is likely minimal given the low rate of dispersal we observed.

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