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Rushing, Clark S.; Marra, Peter P.; and Dudash, Michele R., "Winter Habitat Quality but not Long- distance Dispersal Influences Apparent Reproductive Success in a Migratory Bird" (2016). *Natural Resource Management Faculty Publications*. 220.
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Winter habitat quality but not long-distance dispersal influences apparent reproductive success in a migratory bird

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Abstract. Long-distance breeding and natal dispersal play central roles in many ecological and evolutionary processes, including gene flow, population dynamics, range expansion, and individual responses to fluctuating biotic and abiotic conditions. However, the relative contribution of long-distance dispersal to these processes depends on the ability of dispersing individuals to successfully reproduce in their new environment. Unfortunately, due to the difficulties associated with tracking dispersal in the field, relatively little is known about its reproductive consequences. Furthermore, because reproductive success is influenced by a variety of processes, disentangling the influence of each of these processes is critical to understanding the direct consequences of dispersal. In this study, we used stable hydrogen and carbon isotopes to estimate long-distance dispersal and winter territory quality in a migratory bird, the American Redstart (*Setophaga ruticilla*). We then applied Aster life-history models to quantify the strength of influence of these factors on apparent reproductive success. We found no evidence that male or female reproductive success was lower for long-distance dispersers relative to non-dispersing individuals. In contrast, carry-over effects from the winter season did influence male, but not female, reproductive success. Use of Aster models further revealed that for adult males, winter territory quality influenced the number of offspring produced whereas for yearling males, high-quality winter territories were associated with higher mating and nesting success. These results suggest that although long-distance natal and breeding dispersal carry no immediate reproductive cost for American Redstarts, reproductive success in this species may ultimately be limited by the quality of winter habitat.

Key words: Aster models; breeding dispersal; carry-over effects; deuterium; long-distance dispersal; natal dispersal; seasonal interactions.

INTRODUCTION

For the majority of species, most individuals breed in the vicinity of their natal or previous breeding location, with only a small number of individuals dispersing far beyond the boundaries of their breeding population (i.e., long-distance natal or breeding dispersal; Clobert et al. 2012). Although these long-distance dispersal movement are generally rare, empirical and theoretical research has demonstrated that they can have a large influence on many evolutionary and ecological processes, including local adaptation and speciation (Savolainen et al. 2007), population dynamics (Bohrer et al. 2005), range expansion (Kot et al. 1996), and the response of species to climate change (Higgins and Richardson 1999). As a result, understanding how often (Nathan et al. 2003), how far (Paradis et al. 1998), and under what conditions (Rushing et al. 2015)

long-distance dispersal occurs remain fundamental questions in ecology and evolution.

Given their capacity for large-scale movements, migratory birds are ideally suited for studying the causes and consequences of dispersal. In recent years, migratory birds have become particularly relevant for understanding long-distance dispersal in light of evidence that such events may be a strategy for responding to annual variation in the phenology of breeding resources. Recent studies have supported the hypothesis that individuals do use phenological cues to select their breeding sites. Studds et al. (2008) found that when juvenile American Redstarts (*Setophaga ruticilla*) departed early from their winter grounds they tended to breed at southerly latitudes whereas later departing individuals bred at more northerly latitudes. A subsequent study (Rushing et al. 2015) also found that immigrants to a breeding population of Redstarts were largely of southerly origins in years with early phenology but originated from the north in years with late phenology. Similar patterns have also been observed in European populations of Pied Flycatchers (*Ficedula*

Manuscript received 8 July 2015; revised 4 November 2015; accepted 23 November 2015. Corresponding Editor: W. D. Koenig.
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hypoleuca), with large influxes of morphologically distinct southern immigrants in years with abnormally early spring phenology (Sirkiä et al. 2013) and later migrating males more likely to disperse north than early migrating individuals (Husek et al. 2014). These results suggest that one result of long-distance dispersal is that it synchronizes reproductive efforts with optimal environmental conditions.

However, simply dispersing to a new breeding location does not ensure that an individual will influence ecological and evolutionary processes. Instead, the contribution of long-distance dispersal to these processes also depends on the ability of dispersing individuals to reproduce successfully in their new environmental (i.e., “effective” dispersal). Dispersing individuals may experience reduced reproductive success because of difficulty establishing territories (Forero et al. 1999) and attracting mates (Bensch et al. 1998) or because they are unfamiliar with local breeding conditions (Hansson et al. 2004). Unfortunately, there is no general consensus about the reproductive consequences of long-distance dispersal (Bensch et al. 1998, Shutler and Clark 2003, Hansson et al. 2004), primarily due to the logistical difficulties of documenting these movements in the field (Koenig et al. 1996),

Adding to the logistical difficulties of simply documenting long-distance dispersal events, estimating reproductive consequences of these movements in migratory birds is challenging because the link between dispersal and reproduction may be confounded by winter habitat quality (i.e., carry-over effects). Previous research on American Redstarts has demonstrated that, in addition to driving patterns of long-distance dispersal (Studds et al. 2008, Rushing et al. 2015), winter habitat quality also influences subsequent reproductive success (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009a). As a result, direct comparison of the reproductive success of local and dispersing individuals may incorrectly indicate a reproductive cost to dispersal, when in reality differences were driven by dispersing individuals experiencing lower quality winter habitat than non-dispersers. Likewise, it is possible that the reproductive consequences of winter habitat quality found in previous studies may have been confounded by costs of long-distance dispersal that were unmeasured.

In this study, we used a novel combination of stable hydrogen and carbon isotopes and Aster life-history models (Geyer et al. 2007) to disentangle and quantify the direct reproductive consequences of long-distance dispersal and winter habitat quality in American Redstarts. This approach allowed us to test the following specific predictions: (1) long-distance immigrants have lower reproductive success than local individuals and (2) after accounting for long-distance dispersal, individuals that hold high-quality winter territories have higher reproductive success than individuals from poor-quality winter territories.

METHODS

Study species and study site

From 2009 to 2012, we studied American Redstarts breeding at the Patuxent Research Refuge in Laurel, Maryland, USA (39°04' N, 76°47' W). American Redstarts are long-distance Neotropical migratory songbirds that breed throughout North America and winter in the Caribbean and Latin America (Sherry and Holmes 1997). The 250-ha study area consists primarily of beech-dominated bottomland forests adjacent to the Patuxent River.

Field methods

Starting on 10 April of each year, the site was surveyed every three days from 0600 to 1200 along transects spaced 100 m apart to record any male seen or heard. During each survey, territory boundaries of all males were mapped by following individuals for 10 min or until visual contact was lost and recording their approximate locations on a gridded map of the study site. The arrival date of each male was recorded as the first day in the 3-d survey period that it was recorded. Males were captured in mist nets within 7–10 d of arrival using playback of conspecific song and a decoy adult male in singing posture. Female Redstarts are cryptic during nest building and do not generally respond to conspecific playback. Therefore, most females (68 out of 74) were captured in mist nets while feeding fledglings later in the season. Upon capture, individuals were classified as either yearlings (second-year) or adults (after-second-year) following Pyle et al. (1997), fitted with a unique combination of leg bands, weighed and measured for body size (tarsus length and unflattened wing chord). One tail feather (R3) and the distal 0.3 mm of each middle claw were sampled for stable hydrogen and stable carbon isotope analyses (Appendix S1).

After banding, male territories were surveyed every 3 d to determine whether individuals attracted a female. Males were considered to be mated if a female Redstart was observed on the individual's territory and if mating behaviors (e.g., mate guarding, courtship songs, copulation, or nest building) were observed. For all territories that contained a mated pair, we searched extensively to locate all nesting attempts and monitored nests every 3 d until either nest failure or nestlings were observed. Nests that were lost to abandonment, predation, weather, or otherwise produced no fledglings were considered unsuccessful. Once nestlings were observed in a nest, the nest was monitored daily until nestlings fledged, at which time we recorded the number of fledglings. Redstarts are obligate single brooders (Sherry and Holmes 1997), so once a nest had successfully fledged young, the adults were no longer monitored. This sampling protocol allowed us to record the status of three separate components of reproduction

for each individual: (1) mated status (i.e., mated vs. unmated); (2) if mated, the fate nesting attempts (successful or unsuccessful); and (3) if a nesting attempt was successful, the number of fledglings produced. Extra-pair copulations are common in American Redstarts (Perreault et al. 1997) though we were unable to determine the true father of fledglings in this study. Therefore we restricted our analysis of males to the “apparent” reproductive success (i.e., the number of observed offspring) of each individual.

Quantifying the factors that influence apparent reproductive success

To avoid testing a large number of models with little biological justification, we focused on factors known to influence reproductive success of Redstarts or closely related species:

1. Dispersal status.—To estimate the natal (yearlings) or breeding (adults) dispersal status of individuals in our population, we used stable hydrogen isotopes from feather samples ($\delta^2\text{H}_f$) to probabilistically determine the origin of all unknown-origin individuals in our population (Rushing et al. 2015). We used annual estimates of the local $\delta^2\text{H}_f$ distribution to probabilistically assign all unbanded birds into one of three dispersal categories (southern, local, northern) based on a predefined threshold for correctly classifying individuals as local. To test the sensitivity of our results to the threshold used to classify dispersal status, we carried out the classifications using two progressively stringent thresholds (80% and 90%; see Appendix S1 for further details about inferring dispersal status). To account for both age-specific consequences in reproductive consequences, we included the interaction of dispersal status with age class in our analyses.

2. Winter territory quality.—To infer winter territory quality, we used stable carbon isotope values from claw samples ($\delta^{13}\text{C}$). Stable-carbon isotope signatures of plants in the tropics vary by water availability (Michener and Lajtha 2008), which is positively correlated with the abundance of small, soft-bodied insects (Studds and Marra 2007). As a result, the amount of $\delta^{13}\text{C}$ in tissues can be used as a proxy for habitat quality for insectivorous birds such as Redstarts (Marra et al. 1998), with more negative values indicating wetter, higher quality habitat and more positive values indicating drier, lower quality habitat. To aid in interpretability, we mean-centered $\delta^{13}\text{C}$ so that positive values indicate higher than average habitat quality and negative values indicate lower than average quality. We included the interaction of $\delta^{13}\text{C}$ with age class to model age-specific effects of winter territory quality.

3. Body condition.—Previous research on American Redstarts demonstrated that body condition influences

reproductive success of females but not males (Smith and Moore 2003). To account for the influence of body condition in the female model, we first estimated body size for each individual using a principle component analysis (PCA) based on wing chord and tarsus length, with the first PCA score used as a measure of overall body size (Marra and Holmes 2001). These scores were then regressed against body mass and residuals were used as an estimate of body condition (Marra and Holmes 2001).

4. Year and age effects.—Reproductive success typically increases with age in many birds, including Redstarts (Lozano et al. 1996), and many bird populations show annual variation in reproductive success (Townsend et al. 2013). To account for age effects and annual variation not accounted for by other predictors, we included age class and year in all models.

As described in the introduction, arrival date on the breeding grounds is highly correlated with reproductive success in Redstarts (Marra et al. 1998). However, because the arrival date of males in our population was significantly correlated with $\delta^{13}\text{C}$ values (Pearson's correlation coefficient = -0.25 , $t = -3.5$, $df = 184$, $P < 0.001$) and because we are confident of the causal relationship between these variables, we omitted arrival date from our analysis to avoid colinearity caused by this correlation. Furthermore, because dispersal status was unrelated to both arrival date ($\beta = -0.23 \pm 0.22$, $df = 184$, $P < 0.29$) and $\delta^{13}\text{C}$ (Rushing et al. 2015), we considered the effects of long-distance dispersal independently of effects of arrival date and winter habitat quality.

Statistical analysis: aster life-history models

In many songbird species, the distribution of reproductive success is bimodal, with a structural mode at zero (corresponding to individuals that either failed to acquire a mate or to nest successfully) and a second mode corresponding to the mean number of fledglings for individuals that mated and nested successfully. This mixture of discrete and continuous components is typical of life-history data (Shaw et al. 2008) but the joint distribution of the individual reproductive components (i.e., mating success, nesting success, and number of fledglings) does not follow any parametric distribution and therefore violates the assumptions of standard generalized linear models (Geyer et al. 2007). Furthermore, independent analysis of each component decreases the sample size for later components and prevents conclusions about overall reproductive success (Geyer et al. 2007).

To overcome these issues, we analyzed our data using unconditional Aster models (Geyer et al. 2007), a recently developed method for analyzing life-history data of this nature (see Appendix S1 for details). For our analysis, we described the conditional relationships between the reproductive components using a simple graphical model

(Fig. 1A) and considered mating success and nesting success to be Bernoulli trials and the number of fledglings to follow a 0-truncated Poisson distribution. To test the predictions outlined above, we first fit a “full” model that contained explicit effects of all predictors on the number of fledglings produced by each individual. However, due to the conditional nature of Aster models, the estimates for each predictor propagate back through earlier nodes and thus directly account for differences due to mating and nesting success (Geyer et al. 2007). Because the reproductive success of individuals from mated pairs cannot be considered independent, we fit separate models for males and females. To test the significance of each predictor, we dropped the predictor from the “full” model and then tested the fit of the reduced model using a likelihood ratio test. For predictors that were included in interaction terms, main effects were tested by dropping both the main effect and interactions. To test the sensitivity of our results to the threshold used to classify dispersal status, the models without dispersal status were compared to “full” models based on both the 80% threshold and 90% threshold. All models were fit using the “aster” package (Geyer 2012) in the R statistical language (R Core Team 2013).

Which reproductive components drive reproductive differences?

Although our primary interest was in quantifying the factors that influence overall reproductive success,

determining which reproductive component(s) drive the variation in reproductive success can provide important mechanistic insights into processes that influence reproduction. To determine which components of reproductive success were responsible for the results observed in our “full” model, we fit additional Aster models for each predictor variable that was found to have a significant influence on overall reproductive success. The first of these “component” models included the effects of the predictor of interest only on the probability of mating (“mate” model) and therefore did not account for any reproductive differences caused by nesting success or the number of fledglings. The second component model contained explicit effects on nesting success (“nest” model). The third component model contained explicit effects on the number of fledglings (“fledgling” model). For each component model, any additional predictors that were not of primary interest were kept as effects on the number of fledglings. We also fit a “base” model that did not contain effects of predictors of interest and used likelihood ratio tests (LRT) to compare each component model to the “base” model, with a significant LRT indicating differences in reproductive success up to that component.

Because the “nest” and “fledglings” models account the effects of earlier components, significant LRT tests when compared to the “base” model do not indicate which components are responsible for differences in reproductive success. Therefore, our component analysis

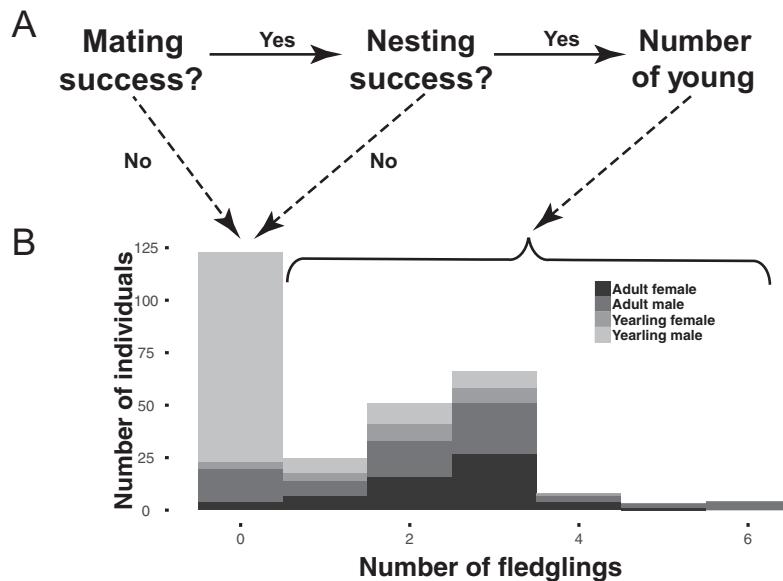


FIG. 1. (A) Graphical model illustrating the relationship between components of reproductive success in our analysis, with solid arrows leading from earlier components (predecessor nodes) to later components (successor nodes). If a predecessor node equals 0 (due to failure to mate or nest successfully), all successor nodes must also equal 0. In our analysis, overall reproductive success is measured as the number of young, conditional on mating and nesting successfully. Mating success and nesting success were modeled as binomial variables and the number of young was modeled as a zero-truncated Poisson variable. (B) Distribution of the reproductive success of all individuals breeding in our study population, measured as the number of fledglings produced by each individual.

included two additional models that contained explicit effects on each component and its successor component (e.g., “mate + nest” and “nest + fledglings”). The single component models were then compared to the more complicated models using LRTs, allowing us to determine whether adding effects on the successor components improved the fit of the single component models.

RESULTS

Between 2009 and 2012, the mean number of fledglings per individual in our study population was 1.37 ± 1.48 (mean \pm SD; range 0–6; $n = 260$), though a large proportion of individuals (47.7%) failed to produce any fledglings, resulting in a strongly bimodal distribution for the number of fledglings (Fig. 1B). The distinct mode at zero was primarily the result of low mating success of yearling males (43.1%, $n = 123$). In contrast, all females (yearling $n = 21$; adult $n = 53$) and virtually all adult males (98.4%; $n = 63$) mated successfully. The remaining zeros were the result of individuals that failed to nest successfully

The “full” Aster models for both males and females confirmed that yearlings had lower apparent reproductive success than adults (Table 1), with yearling males producing on average 80% fewer fledglings than adult males (yearling males, 0.43 ± 0.08 fledglings; adult males, 2.05 ± 0.26 fledglings) and yearling females producing on average 26% fewer fledglings than adult females (yearling females, 1.75 ± 0.29 fledglings; adult females, 2.38 ± 0.24 fledglings). The Aster analysis also revealed a strong year effect for yearling males, with higher apparent reproductive success in 2010 and 2012 than in 2009 and 2011 (Table 1).

Depending on the odds ratio used to classify dispersal status, stable hydrogen isotope data indicated that approximately 6–14% of the 260 individuals included in our analysis were long-distance dispersers (Rushing et al. 2015). Contrary to our prediction, neither natal nor breeding dispersal status was a significant predictor of apparent reproductive success for either sex (Table 1; Appendix S2: Figs. S1 and S2) and likelihood ratio tests indicated no significant dispersal \times age class interaction for either sex (males, $\chi^2 = 0.17$, $df = 2$, $P = 0.92$; females, $\chi^2 = 0.23$, $df = 1$, $P = 0.63$).

TABLE 1. Factors influencing apparent reproductive success in American Redstarts.

Factors	Estimate	<i>z</i>	χ^2	df	<i>P</i>
Males, $n = 186$					
Age class	1.76 ± 0.64	2.75	53.42	1	<0.001
Origin					
Local	0.07 ± 0.22 (-0.16 ± 0.29)	0.27 (-0.55)	1.82 (0.37)	2	0.40 (0.83)
Southern	0.29 ± 0.34 (-0.25 ± 0.44)	-0.82 (-0.57)			
Winter habitat quality	0.42 ± 0.12	3.51	13.01	1	<0.001
Year					
2010	-0.35 ± 0.21	-1.63	2.52	3	0.47
2011	0.19 ± 0.22	0.87			
2012	-0.15 ± 0.19	-0.76			
Year \times Age class					
2010	1.39 ± 0.68	1.78	13.65	3	0.003
2011	0.08 ± 0.73	0.12			
2012	1.05 ± 0.66	1.58			
Females, $n = 74$					
Age class	0.46 ± 0.22	2.07	4.63	1	0.03
Origin					
Local	0.05 ± 0.39 (0.03 ± 0.40)	0.127 (0.08)	0.117 (0.69)	2	0.943 (0.72)
Southern	-0.19 ± 0.78 (0.61 ± 0.79)	-0.24 (0.77)			
Winter habitat quality	-0.008 ± 0.19	-0.04	0.002	1	0.97
Body condition	-0.12 ± 0.18	-1.24	1.56	1	0.21
Year					
2010	0.06 ± 0.25	0.24	2.93	3	0.40
2011	0.40 ± 0.24	1.66			
2012	-0.06 ± 0.24	-0.24			

Notes: Coefficient estimates \pm SE are from the “full” unconditional Aster models. χ^2 , df, and *P* values refer to the likelihood ratio test (LRT) test used to compare the reduced model to the full model. For dispersal status, values outside parentheses are based on the 80% threshold and values inside parentheses are based on the 90% threshold. Age class and year treated yearlings and the year 2009 as dummy variables, respectively. Interaction terms that were not significant were dropped and are not displayed here. Values in boldface type indicate predictor variables that were significant at the 0.05 level. LRT statistics for main effects that are included in interaction terms are based on removing both the interaction and main effects.

Consistent with our predictions, winter territory quality had a significant impact on overall apparent reproductive success of males (Table 1, Fig. 2). Based on estimates from the “full” model for males, males of both age classes from the lowest quality winter habitat suffered a nearly 90% reduction in apparent reproductive success compared to individuals from the highest quality habitat (Fig. 2). However, contrary to our predictions, winter habitat quality did not influence apparent reproductive success in females, nor did body condition (Table 1).

Which reproductive components drive reproductive differences?

Because we did not find evidence that winter habitat quality, dispersal status, or body condition influenced female apparent reproductive success, we limited our analysis of reproductive components to males only.

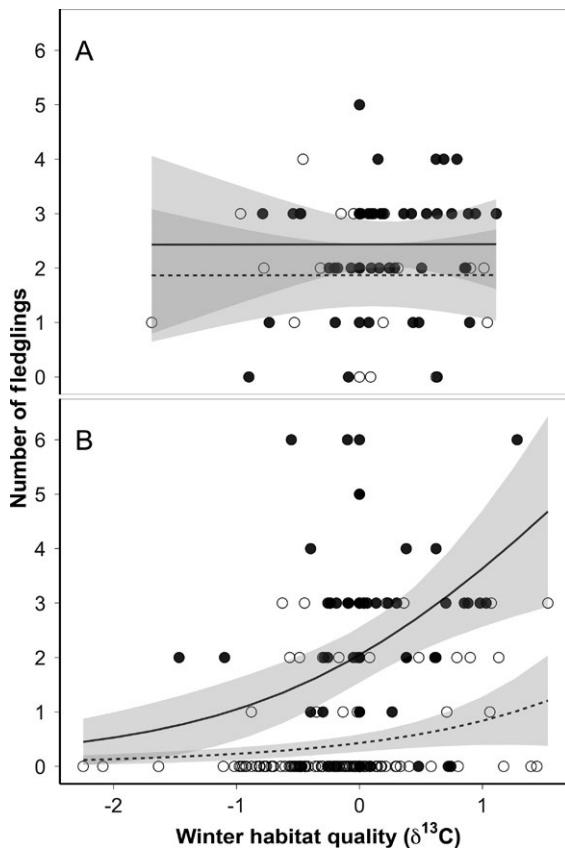


FIG. 2. Apparent reproductive success of (A) female and (B) male American Redstarts as a function of winter territory quality ($\delta^{13}\text{C}$) based on the “full” Aster model and assuming individuals originated locally. $\delta^{13}\text{C}$ values were mean centered previous to analysis. Positive values indicate better than average winter habitat quality and negative values indicate less than average habitat quality. For each sex, solid circles/solid lines show the observed/predicted number of fledglings for adults and open circles/dotted lines show the observed/predicted number of fledglings for yearlings. Gray ribbons show the 95% confidence intervals.

TABLE 2. Aster life-history analysis to determine which components of male apparent reproductive success are influenced by winter habitat quality.

Model	Model deviance	Model df	Test deviance	Test df	P
Adults, n = 63					
Base	57.89	3			
Nest	57.78	4	0.11	1	0.74
<i>Fledglings</i>	<i>54.16</i>	<i>4</i>	<i>3.74</i>	<i>1</i>	<i>0.05</i>
Nest + Fledglings	53.07	5	4.71	1	0.03
Yearlings, n = 123					
Base	258.99	6			
Mate	253.59	7	5.39	1	0.02
Nest	250.07	7	8.92	1	0.003
Fledglings	251.05	7	7.94	1	0.004
Mate + Nest	249.46	8	4.14	1	0.04
Nest + Fledglings	249.59	8	0.48	1	0.48

Notes: Each model contains explicit effects on winter territory quality on only the reproductive component(s) indicated by the model name. For a full description of the models, see *Methods*. Test statistics for each model show the results of a likelihood ratio test (LRT) comparing that model to a nested model that included explicit effects of winter territory quality only on earlier reproductive components. A significant result indicates that the reproductive component(s) given in the name of the model were significantly influenced by winter territory quality. Models shown in boldface type were significant at the 0.05 level and models shown in italic typeface were significant at the 0.1 level.

Furthermore, because all but one adult male acquired a mate, we restricted our adult male component analysis to nesting success and number of fledglings.

Based on the results of our full model for male reproductive success, our component analysis for adult males included only the influence of winter territory quality, leading to four models (Table 2). As expected, the “fledglings” model for adult males indicated an effect of winter habitat quality on the number of fledglings (Table 2). In contrast, comparison of the “nest” model to the “base” indicated that winter habitat quality did not influence nesting success in adult males (Table 2). This conclusion is supported by the fact that adding explicit effects on the number of fledglings significantly improved the fit of the “nest” model (Table 2). Thus, our results indicate the winter territory quality drives variation in apparent reproductive success of adult males through its influence on the number of fledglings rather than through intermediate effects on mating and fledging success.

For yearling males, the “full” model indicated that both winter territory quality and year influenced apparent reproductive success. Because our primary interest was on the influence of winter territory quality and not year, we fit six component models that included explicit year effects on the number of fledglings but differed in which component was influenced by winter territory quality. Comparison of the “mate” model to the “base” model uncovered a clear effect of winter territory quality on mating success (Table 2), indicating that yearling males from high-quality winter territories

were more likely to acquire a mate than individuals from low-quality winter territories (Fig. 3A). Adding explicit effects on nesting success further improved model fit (Table 2), indicating that even once the effects of mating success are accounted for, yearling males from high-quality winter territories were more likely to nest successfully than individuals from low-quality territories (Fig. 3B). This conclusion is supported by the significantly better fit of the “nest” model compared to the “base” model (Table 2). As expected, the “fledglings” model revealed a clear impact of winter habitat quality on the number of fledglings produced but adding explicit effects on the number of fledglings did not improve the fit compared to the “nest” model

(Table 2). These results indicate that once the effects on mating and nesting success are accounted for, winter territory quality had no further influence on the number of fledglings produced by yearling males.

DISCUSSION

Long-distance dispersal is a fundamental process in ecology and evolution but whether these movements carry reproductive costs remains poorly understood. In this study, we used a combination of stable isotope analysis and novel analytical methods to disentangle the reproductive consequences of breeding-season dispersal and winter season events in a migratory songbird. Contrary to our predictions, we found no reproductive costs to long-distance natal or breeding dispersal for either sex. Although these results appear to contradict previous studies that found long-distance dispersal reduced lifetime reproductive success in several migratory bird species (Wheelwright and Mauck 1998, Shutler and Clark 2003; Hansson et al. 2004, Nevoux et al. 2013), none of these studies found an immediate influence of long-distance dispersal on apparent fecundity.

Although we did not find evidence that apparent reproductive success differed between immigrants and local individuals, several caveats could influence this conclusion. First, our analysis was restricted only to individuals that had successfully dispersed and it remains possible that long-distance dispersal may influence overall fitness if dispersers suffer lower survival than non-dispersers. Recent work on migratory birds indicates that the probability of surviving migration decreases with increasing migration distance (Sanz-Aguilar et al. 2012), suggesting that the survival costs of long-distance dispersal may be indirectly influenced by mortality experienced during migration. Second, extra-pair copulations are common in Redstarts (Reudink et al. 2009b) and there is evidence that immigrant males are more likely to be cuckolded than local males (Perreault et al. 1997). If true in our population, immigrant males may father a lower proportion of their fledglings, reducing realized reproductive success compared to local individuals. Because female Redstarts typically raise only their own offspring (Perreault et al. 1997), the prevalence of extra-pair copulations is unlikely to influence our conclusions about long-distance dispersal and female reproductive success. Third, there is evidence from other passerines that offspring of immigrant pairs may suffer lower survival than offspring from local pairs (Doligez and Pärt 2008). Although we were unable to track the performance of offspring in our study population, immigrant Redstarts may have suffered lower lifetime reproductive success than local individuals if their offspring suffer lower survival than those of local pairs (Wheelwright and Mauck 1998, Hansson et al. 2004). Further research, particularly experimental manipulations, on the relationship between dispersal, extra-pair copulations, and

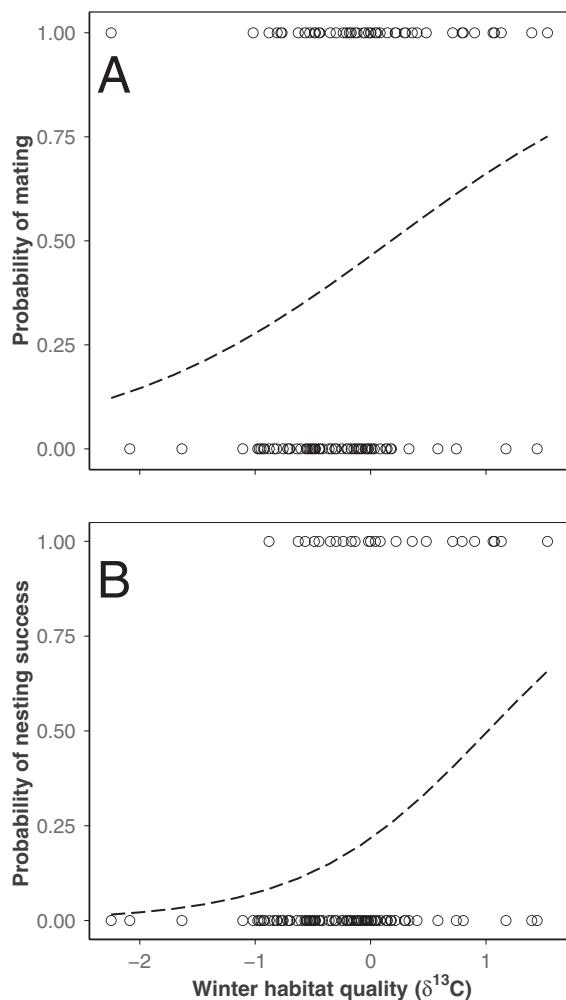


FIG. 3. Probability of (A) acquiring a mate and (B) successfully nesting for yearling males as a function of winter territory quality ($\delta^{13}\text{C}$) based on the “mate” and “fledge” component models and assuming individuals originated locally. $\delta^{13}\text{C}$ values were mean centered previous to analysis. Positive values indicate better than average winter habitat quality and negative values indicate less than average habitat quality. Open circles show the observed mating and nesting success. Gray ribbons show the 95% confidence interval.

offspring survival are needed to unravel these complex interactions.

Contrary to our prediction, we found no evidence that winter territory quality influenced female apparent reproductive success. Although surprising, this result does not necessarily indicate that carry-over effects from the winter season are unimportant for female fitness. First, previous research on other Redstart populations has found evidence that winter habitat quality influences female reproductive success (Norris et al. 2004). This discrepancy may be due to the fact that females in our study were captured once fledglings had left the nest. By this time in the breeding season, nail tissues may have incorporated $\delta^{13}\text{C}$ values from the breeding grounds, which could have reduced our ability to accurately detect the influence of winter territory quality on reproductive success. Second, carry-over effects from the winter season may operate over larger spatial scales than individual territories (Rushing et al. 2015) or on fitness traits other than reproductive success (e.g., survival; Studds and Marra 2005). Thus, carry-over effects are likely to be important for driving breeding demography of females, despite our inability to detect effects in this study.

For males, habitat quality experienced during the preceding winter, but not long-distance dispersal, strongly influenced the apparent reproductive success. The influence of winter habitat quality on adult male reproductive success is consistent with previous research on American Redstarts (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009a). However, the novel use of Aster models revealed new mechanisms by which carry-over effects from the winter season influence reproductive success in yearling males. For these individuals, high-quality winter habitat was associated with both higher mating success and higher nesting success than low-quality habitat. However, once these differences were accounted for, winter habitat had no further influence on the number of fledglings. Although many factors could explain these results, we suggest that the reproductive differences within and between age classes are due to differences in arrival time and individual quality (McKellar et al. 2013).

In Redstarts and many other songbirds, early arrival on the breeding grounds is associated with increased access to potential mates and high-quality territories (Aebischer et al. 1996, Lozano et al. 1996), and higher nesting success (Grant et al. 2005). Thus, winter habitat may influence reproductive differences primarily by driving variation in arrival date (Marra et al. 1998). Indeed, among males in our population, winter territory quality was highly correlated with arrival date and arrival date was a strong predictor of the number of fledglings produced (-0.60 ± 0.07 [estimate \pm SE], $z = -9.12$, $P < 0.001$). However, if arrival timing was the primary driver of the age-specific differences revealed by our Aster analysis, then we would further predict that arrival date should be correlated with mating

success and nesting success for yearling males, which was not the case (mating success, -0.18 ± 0.25 , $z = -0.73$, $P = 0.47$; nesting success, -0.14 ± 0.31 , $z = -0.46$, $P = 0.65$). Thus, arrival date alone does not explain the relationship between winter territory quality and reproductive success in yearling males.

An alternative to the arrival-timing hypothesis is that variation in reproductive success is determined by differences in individual quality (McKellar et al. 2013). Both within and between age classes, high-quality individuals are expected to acquire the best breeding (Leniowski and Wegrzyn 2013) and winter territories (Marra and Holmes 2001), attract females (Lozano et al. 1996), and nest successfully (Saino et al. 2012). In our population, the higher mating success, nesting success, and total reproductive success of adult males compared to yearling males supports the hypothesis that adults are generally higher quality mates than yearlings (Lozano et al. 1996). For yearling males, the significant relationship between winter territory quality and mating and nesting success (Fig. 3) and the lack of relationship between arrival date and these components further supports the hypothesis that variation in reproductive success is determined primarily by individual quality. We suggest that yearling males able to hold high-quality winter territories are competitively dominant to the yearlings that were forced into low-quality habitat (Marra 2000) and these individuals may be more attractive to females (Reudink et al. 2009b), and may also be better at defending nests. These predictions and our results are consistent with McKellar et al. (2013), who used experimental manipulations to show that reproductive success of Redstarts was a function of arrival date and individual quality.

Quantifying the consequences of long-distance dispersal and winter habitat quality are critical to understanding if and how migratory species will respond to global climate change. Although a large number of studies have focused on the impacts of advancing temperate phenology (Møller et al. 2008, Saino et al. 2011), climate change is also predicted to result in decreased precipitation in many of the tropical areas inhabited by migratory birds during their winter period (Neelin et al. 2006). Our results indicate that this long-term decline in winter habitat quality may have a larger impact on the reproductive success of migratory birds than advances in resource phenology caused by temperate warming and highlight the importance of accounting for the full annual cycle when considering the vulnerability of migratory birds to climate change (Small-Lorenz et al. 2013).

ACKNOWLEDGMENTS

Funding was provided by the COSMOS Foundation, the American Ornithologists Union, the Washington Biologists Field Club, the Maryland Ornithological Society and the National Science Foundation. C. S. Rushing was supported by the BEES/BISI program, a Wiley Dissertation Fellowship from

the University of Maryland, and a Smithsonian Institution Pre-doctoral fellowship. We thank C. Fenster, C. Geyer, and R. Reynolds for statistical help and comments from S. Sillett, W. Fagan, D. Gruner, D. Hawthorne, W. Koenig, and two anonymous reviewers.

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