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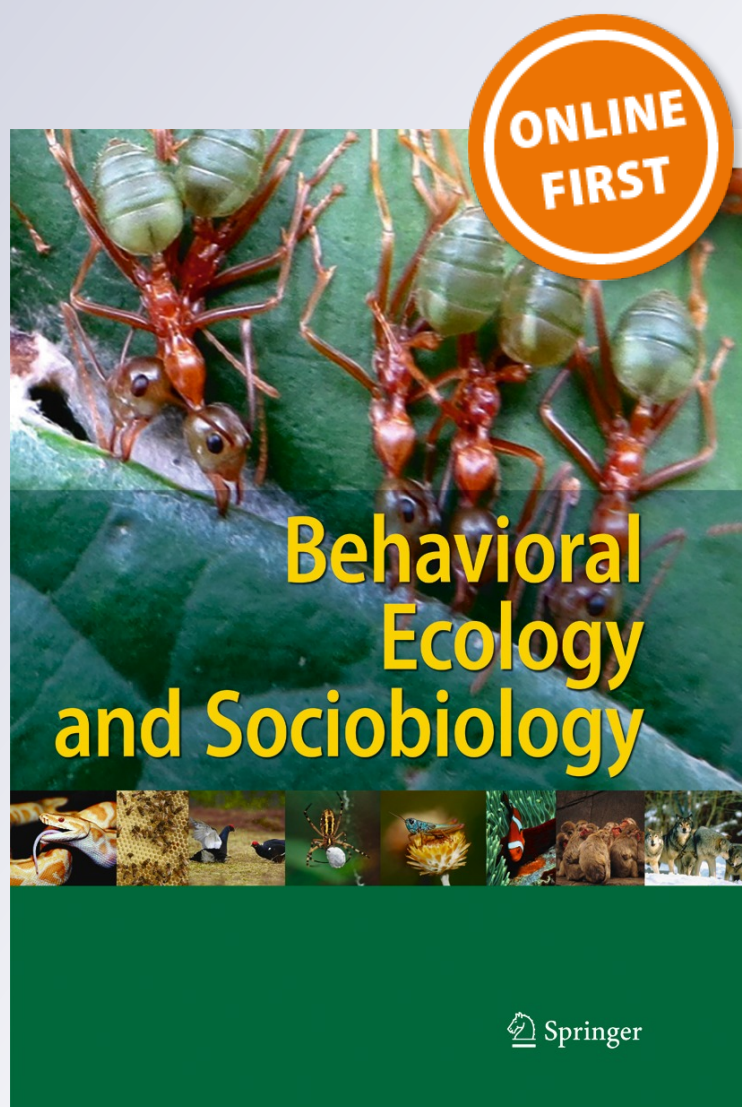
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Divergent oviposition preferences of sister species are not driven by nest survival: the evidence for neutrality

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Abstract Both adaptive and neutral trait evolution can contribute to divergence, but the relative contributions of the two remain unclear. Oviposition preference, a trait that has been demonstrated to contribute to divergence among populations, is often presumed to be an adaptive trait. Few studies explicitly test this assumption, however, and several researchers have demonstrated non-adaptive oviposition preferences in wildlife populations. In this study, we test whether adaptive divergence can explain current differences in the oviposition preferences of two sister species. In 2012 and 2013, we conducted a demographic study of sympatrically breeding populations of two sparrow species (*Ammodramus caudacutus* and *Ammodramus nelsoni*) and measured vegetation characteristics at nest and non-nest points. We found evidence for oviposition preference in both species and significant differences between the species' preferences. The vegetation characteristics that vary between species did not predict nest survival or offspring production, however. Our results provide an example of oviposition preference at a population level that appears non-adaptive as measured by productivity. We discuss

other mechanisms by which oviposition preference can be adaptive, and make a case for the role of neutral evolution in shaping the oviposition preferences of these species. If divergence in oviposition preference is at least periodically neutral, as we hypothesize, such differences could provide fodder for future adaptation or reproductive isolation among populations.

Keywords Non-adaptive · Neutral evolution · Oviposition preference · Nest site selection · Speciation · Sympatry · Saltmarsh sparrow · Nelson's sparrow

Introduction

Both adaptive and neutral trait evolution can contribute to divergence among populations, but the relative contributions of the two mechanisms remain unclear. Though genetic drift is acknowledged to contribute to divergence between populations in allopatry (Lenski and Travisano 1994; Gavrillets 2003; Papke et al. 2003; Coyne and Orr 2004; Petren et al. 2005; Comes et al. 2008), much work on sympatric speciation centers on selective forces promoting divergence, such as in the model stickleback system (Rundle et al. 2000; Coyne and Orr 2004). However, some authors argue that most evolution is neutral or nearly so. They suggest that populations evolve along relatively flat planes within a highly dimensional niche space and have demonstrated these results with modeling experiments (Kimura 1983; Gavrillets 2003, 2004).

Oviposition preference, specifically where an organism chooses to lay and keep its eggs, has been observed to contribute to divergence and is often presumed to be adaptive. Oviposition preference has contributed to divergence among populations in a wide range of taxa (Brykov et al. 1996; Etges 1998; Hawthorne and Via

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2001; Friesen et al. 2007). In fact, the most convincing cases of sympatric speciation in animals are related to divergence in oviposition preferences (Sorenson et al. 2003; Coyne and Orr 2004; Machado 2005; Rønsted et al. 2005; Althoff et al. 2006). Oviposition preference is often presumed adaptive for good reason; it can dramatically affect individual fitness via both fecundity (Resetarits 1996) and adult survival (Scheirs et al. 2000; Spencer 2002; Miller et al. 2007). Many ecological studies, however, presume oviposition preference is adaptive without explicitly testing for a relationship between oviposition behaviors and fitness (Arlt and Pärt 2007).

In a review of bird nest site preferences, Clark and Shutler (1999) found that only 54 % of oviposition studies related preferences to nest success and only 10 % of studies examined found evidence for adaptive oviposition preference. Finally, several researchers who have explicitly examined the relationship between oviposition preference and fecundity across a wide range of taxa have reported oviposition preferences that are not adaptive (review—Robertson and Hutto 2006; birds—Dwernychuk and Boag 1972; Filliater et al. 1994; Arlt and Pärt 2007; Chalfoun and Schmidt 2012; insects—Rausher 1979; Thompson 1988; Kriska, Horváth, and Andrikovics 1998; Ries and Fagan 2003; reptiles—Kamel and Mrosovsky 2005).

There are many reasons why oviposition preference, or any trait that impacts fitness, can be non-adaptive. In this study, we define non-adaptive as a trait that does not increase an organism's fitness. This definition includes both neutrality and maladaptation. A characteristic is neutral if it confers no benefit or disadvantage to its carrier, whereas a trait is maladaptive if it decreases an organism's fitness. Gould and Lewontin's (1979) classic "non-exhaustive list" of causes for lack of adaptation includes evolutionary constraints, methodological shortcomings, and neutral evolution. It is important to understand the non-adaptive forces behind the evolution and divergence of oviposition preferences because differences in these traits appear to be important for multiple modes of speciation (e.g., allopatric, sympatric, and ecological).

In this study, we explicitly test for adaptive differences in the oviposition preferences of two Emberizid sparrows, saltmarsh (*Ammodramus caudacutus*) and Nelson's (*Ammodramus nelsoni*) sparrows. These sister species are known collectively as sharp-tailed sparrows. Together, they provide an exemplary study system for exploring the adaptive versus non-adaptive evolution of oviposition preferences because their distinctive life history sets the stage for non-adaptive divergence in a number of ways.

First, the characteristics of the tidal marsh where sharp-tailed sparrows breed may weaken selective pressure. Bayard and Elphick (2010) observed that saltmarsh sparrow nest placement was spatially random in Connecticut, and they suggested this random nest placement developed as a result of a lack of opportunity for adaptation. Female sharp-tailed sparrows nest a few centimeters above the ground in the high marsh zone, which is characterized by flooding events each month (Tiner 2013). As a result, the majority of sharp-tailed sparrow nest failure is isolated in time, but spatially widespread. The spatial homogeneity of nest failure in tidal marshes thus leaves little meaningful variation in oviposition preference upon which selection can act. Previous research supports this hypothesis; saltmarsh sparrow oviposition preferences have not been predictive of nest success in multiple studies of the species across New England (Gjerdrum et al. 2005; Shriver et al. 2007).

Second, the evolutionary history and breeding biology of sharp-tailed sparrows eliminate many mechanisms that would cause adaptive trait evolution. There is no evidence for competitive exclusion between these species. Males and females of both species are non-territorial, and the home ranges of both species overlap widely with both conspecifics and heterospecifics (Greenlaw and Rising 1994; Shriver et al. 2011). Because males of both species do not contribute parental care, oviposition preferences and female fecundity are not constrained by territory availability, dominance hierarchies, or male behavior. Given their overlapping home ranges, similar mating systems, and the spatial homogeneity of nest failure, saltmarsh and Nelson's sparrows breeding in sympatry are subject to similar, if not equivalent, local selection for oviposition preference.

Finally, evolutionary and developmental constraints are unlikely to be the cause of divergence between the taxa. As sister species that became reproductively isolated as recently as 600,000 years ago (Rising and Avise 1993), saltmarsh and Nelson's sparrows share most of their evolutionary history and the accompanying phylogenetic constraints. The two species also interbreed readily where their ranges overlap (Greenlaw and Rising 1994; Walsh et al. 2011), illustrating that they share most developmental constraints. Through the process of elimination, we are left with genetic drift as one of the most likely drivers for the development, or at least maintenance, of divergence in oviposition preferences.

In this study, we use sympatrically breeding populations of sharp-tailed sparrows as a case study to investigate selection versus drift as major drivers of divergence in oviposition preferences. We first confirm whether, consistent with previous studies, sharp-tailed sparrows exhibit oviposition preferences. We then test whether oviposition preference differs between saltmarsh and Nelson's sparrows with broadly overlapping home

ranges. Finally, we test whether any observed differences in oviposition preference between the species are positively related to fecundity and therefore are potentially adaptive.

Methods

Study site and field methods

We compared oviposition preferences of saltmarsh and Nelson's sparrows in Scarborough Marsh, Cumberland County, Maine, USA, located in the sympatric sharp-tailed sparrow range (Hodgman et al. 2002). We surveyed two, 10-ha study sites that are separated by 2.5 km, including a wide river and active train tracks. In 2 years of study, we have captured over 450 unique individuals, only one of which was captured at both of these study sites. Thus, we consider the populations to be largely independent.

We searched for nests once or twice per week from May through August, 2012–2013. Following discovery, we revisited nests every 1 to 3 days until the nesting attempt was completed via fledging or failure. We captured attending females at the nest site with mist nets to determine species. Each female was uniquely marked with a numbered aluminum leg band from the United States Geological Survey to track multiple nesting attempts throughout the breeding season and across multiple years.

In Scarborough Marsh, saltmarsh and Nelson's sparrows interbreed readily. Based on morphology, they exhibit a gradient of introgression. Genetic analysis of sharp-tailed sparrows captured in northern New England indicates high levels of introgression, suggesting that the species have interbred extensively (Rising and Avise 1993; Shriver et al. 2005; Walsh et al. 2011). Samples collected in southern Maine in the late nineteenth century show characteristics of hybridization, suggestive that the species have interbred at our study site for at least 150 years (KJR unpublished data).

Because of the extensive introgression between these species, we treated species as a continuous variable as measured by plumage (sensu Shriver et al. 2005) rather than using a binary species assignment. For each of 13 plumage characteristics (e.g., color and definition of breast streaking, width of crown stripes), we assigned each adult sparrow a score ranging from 1 to 5. Low scores represent traits typical of Nelson's sparrows, while high scores represent traits typical of saltmarsh sparrows. The scores in the 13 categories are then summed to produce an integrated species index ranging from 13 to 65. Previous studies have found general concordance between plumage and genetic hybrid status (Shriver et al. 2005; Walsh et al. 2015). To minimize observer subjectivity, we averaged the summed

plumage score of each female across all captures within a single breeding season.

At each nest site, we measured 16 characteristics. These included four characteristics of the built nest structure and 12 vegetation characteristics within a square 1-m² plot centered on each nest. Nest structure measurements included total nest height (lip of nest bowl to ground), nest depth, distance from bottom of the nest to the ground, and amount of nest canopy as measured by estimating the percentage of the nest bowl that was visible through the canopy while viewing the nest from directly above. For vegetation characteristics, we measured thatch depth and maximum vegetation height, and we visually estimated average vegetation height at the center (at the nest) and midpoints of the 1-m² plot sides. We also visually estimated percent cover of all species present within the 1-m² plot (Table 1), with all cover classes summing to 100 %. We chose characteristics based on previous research on sharp-tailed sparrows (Gjerdrum et al. 2005; Shriver et al. 2007) and the predominant vegetation at our site (Table 1).

We recorded the four nest structure characteristics upon discovery of the nest and the remaining vegetation characteristics upon nest completion (fledging or failure) to minimize disturbance to the nesting female. We measured the same suite of vegetation structure and cover characteristics within a 1-m² plot centered at non-nest points that we randomly selected within the study sites using the "Create Random Points" tool in the "Data Management" toolbox of ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, USA). We surveyed non-nest points throughout the breeding season, within a week of the completion of a paired nest site to control for plant phenology over the study period. We excluded randomly selected points that were located in standing water during field surveys.

Statistical analysis

Statistical analyses were performed using R 3.0.2 (R Core Team 2014). We first used a multiple analysis of variance to test whether sharp-tailed sparrows as a whole exhibit an oviposition preference as measured by 12 vegetation characteristics (Table 1). We used one-way analyses of variance to identify whether mean vegetation characteristics differed significantly between nest and non-nest points. To ensure that both species exhibit a preference, we performed a multiple analysis of variance on saltmarsh and Nelson's sparrows separately as well. We separated the dataset into two subsets based on plumage score limits. We defined saltmarsh sparrows as females with summed plumage scores of 45 or greater, which is the 95th percentile of birds captured in Connecticut. This is the closest breeding population outside of the hybrid zone where we collected plumage score data (Hodgman et al. 2002; Walsh et al. 2011). We defined Nelson's sparrows as females with a summed plumage score of 31 or less based on the limit

Table 1 Vegetation characteristics (mean±SD) at nest and non-nest points in current and previous studies of sharp-tailed sparrows in New England saltmarshes, USA

Vegetation characteristic	Nest site	Non-nest point	<i>P</i> value	Gjerdrum (2005) ^a	Shriver (2007) ^b
Thatch depth at 1-m ² quadrat midpoints (cm)	9.2±3.7	6.4±4.4	<0.001	–	sig.
Thatch depth at center (cm)	16.3±5.7	6.9±6.0	<0.001	sig.	–
Maximum vegetation height at 1-m ² quadrat midpoints (cm)	54.3±10.7	45.8±13.8	<0.001	sig.	–
Maximum vegetation height at center (cm)	61.7±12.4	46.3±15.4	<0.001	–	–
Average vegetation height at 1-m ² quadrat midpoints (cm)	37.5±8.9	33.7±11.6	<0.01	–	–
Average vegetation height at center (cm)	41.4±9.9	33.6±12.6	<0.001	–	–
Water (% cover)	2.2±5.7	3.7±12.5	0.29	–	–
<i>Spartina patens</i> (% cover)	56.2±26.2	33.9±37.9	<0.001	sig.	sig.
<i>Spartina alterniflora</i> (% cover)	27.4±24.4	22.1±30.4	0.15	non-sig.	non-sig.
<i>Distichlis spicata</i> (% cover)	9.9±20.3	9.8±19.9	0.97	sig.	non-sig.
<i>Juncus gerardii</i> (% cover)	1.8±9.3	10.6±24.7	0.01	sig.	non-sig.
Other species (% cover)	1.8±5.2	17.4±28.1	<0.001	–	–

The means shown are averages among the midpoints of four sides on a 1-m² quadrat. For the present study, we show mean±standard deviation of vegetation characteristics for nest site and non-nest points. Reported *P* values are derived from post hoc one-way comparisons of variance between nest and non-nest points. We also include indications of vegetation characteristics found to be significantly related to nest sites in these species in previous studies. Dashes indicate that a characteristic was not measured in the previous study.

^a Gjerdrum et al. (2005)

^b Shriver et al. (2007)

established by Shriver et al. (2005). Hybrids were thus excluded from both subsets of data. We tested for oviposition preferences in both species with the full analysis of variance model on each of these subsets.

We then created a general linear model to test whether the species identity of nesting females (as measured continuously by summed plumage score, using all females) covaried with the same 12 vegetation characteristics and four additional nest characteristics. We also included covariates to control for year and study site. We used stepwise AIC model selection (R package MASS, Ripley et al. 2014) to choose the most parsimonious suite of nest and vegetation characteristics that predicted the species of nesting females as measured by summed plumage score.

Finally, we modeled the relationship between the vegetation characteristics that best predicted species of a nesting female and two estimates of fecundity, daily nest survival probability, and brood size (number of nestlings produced by a successful nest). First, we used the program MCEstimate to generate daily nest survival probabilities. MCEstimate estimates daily nest survival probabilities similarly to the logistic exposure method (Mayfield 1975; Dinsmore et al. 2002; Rotella et al. 2004; Shaffer 2004), but within a Markov-Chain framework (Environmental Protection Agency Mid-continent Ecology Division, Duluth, USA; see Etterson et al. 2007, 2014; Jackson et al. 2011). For all nests, we estimated daily nest survival probability as a function of year and the vegetation characteristics from the top model for distinguishing among species as measured by summed plumage score from

the previous step. We created a null model in which daily nest survival rate was held constant among all nests. We compared the top model to the null model using Akaike's Information Criterion (Akaike 1974; Burnham and Anderson 2002) to test whether differences in oviposition preferences can lead to differences in nest survival between saltmarsh and Nelson's sparrows. To estimate local variation in nest survival, we also used MCEstimate to estimate daily nest survival rate as a function of study site. Second, we used a Poisson regression to estimate brood size, an alternate estimate of fecundity, as a function of year and the nine vegetation characteristics from the top model for distinguishing among species as measured by summed plumage score (R base package, R Core Team 2014).

Finally, we created two Poisson regression models to test for differences in additional fecundity parameters along the species gradient as measured by summed plumage score. In separate models, we estimated number of nesting attempts and clutch size as functions of the summed plumage score of associated females (R base package, R Core Team 2014). Goodness-of-fit tests indicated that for brood size, clutch size, and number of nesting attempts, the data fit the assumptions of Poisson regressions.

Results

We compared vegetation characteristics at 190 randomly selected points to 92 sharp-tailed sparrow nest sites. Of these,

27 nest sites were chosen by Nelson's sparrow females, 47 by saltmarsh sparrows, and 18 by females within the hybrid range according to the plumage limits described. With a total of 1159 exposure days, we observed daily nest survival probabilities of 0.9402 ± 0.01 (mean \pm SE; $n=33$ nests) and 0.9486 ± 0.01 (mean \pm SE; $n=59$ nests) by study site.

Vegetation structure and cover characteristics reliably distinguished between nest and non-nest points (Table 1; $n=282$, approximate $F=18.7_{12,269}$, $P<0.001$). This pattern persisted in the subsets of data that included only saltmarsh ($n=47$ nests and 47 randomly selected points; $F=8.6_{12,81}$, $P<0.001$) and Nelson's sparrows ($n=27$ nests and 27 randomly selected points; $F=4.6_{12,41}$, $P<0.001$), demonstrating that both species exhibit an oviposition site preference. We found that nine of the vegetation characteristics examined had population means that significantly differ between nest and non-nest points (Table 1).

Our results also indicated that nest and vegetation characteristics varied across the sharp-tailed sparrow species gradient ($n=92$, $R^2=0.28$, $F=3.1_{17,74}$, $P<0.001$; Table 2). The best model included nine of the 16 measured nest and vegetation characteristics and the year covariate ($n=92$, $R^2=0.33$, $F=5.5_{10,81}$, $P<0.001$). The best model did not include study site, indicating that nest site preferences did not vary based on local habitat availability.

Using year and the nine characteristics included in the best model for predicting species as measured by summed plumage score, oviposition site did not predict daily nest survival probability (Table 3). The nest characteristics that best predicted species performed worse than the null model for predicting daily nest survival probability ($\Delta AIC_c=+3.14$, model weight=0.17). Using year and the nine characteristics included in the best model for predicting species, oviposition site also did not predict brood size ($\chi^2(10, n=30)$, $P=0.82$).

Individual females nested an average of 1.26 ± 0.06 times per year (mean \pm SE; $n=73$). Mean clutch size across all nests was 3.65 ± 0.09 eggs or nestlings per nest (mean \pm SE; $n=92$). Among successful nests, mean brood size was 2.53 ± 0.19

nestlings per nest (mean \pm SE; $n=30$). We found no evidence that number of nesting attempts ($\chi^2(71, n=73)$, $P=0.50$) or clutch size ($\chi^2(92, n=90)$, $P=0.61$) varied by species as measured by summed plumage score.

Discussion

Differences in oviposition preference have been often cited as mechanisms of reproductive isolation and a driver of ecological speciation between sister taxa (Coyne and Orr 2004; Nosil 2012). However, we demonstrate evidence of sympatric sister taxa with oviposition preferences that are divergent but appear not to be under current selection pressure for maximizing nest survival. Alternative mechanisms for maximizing fitness via oviposition site exist. We present multiple lines of evidence that suggest that variation in oviposition site between Nelson's and saltmarsh sparrows is maintained despite a lack of selective pressure, however.

Similar to the two previous studies that examined small-scale nest-site preference in sharp-tailed sparrows, we found that both saltmarsh and Nelson's sparrows breeding in Scarborough Marsh exhibit oviposition preferences (Table 1). Previous studies and our own found that both structural and vegetation cover characteristics were important in distinguishing between nest and non-nest points (Gjerdrum et al. 2005; Shriver et al. 2007). Moreover, the characteristics in our best model were similar to those reported by previous studies. For example, our results agree with those of both Gjerdrum et al. (2005) and Shriver et al. (2007), who also found that nest sites were positively associated with percent cover of *Spartina patens* and exhibited a deeper thatch layer compared to randomly selected non-nest points. The Gjerdrum et al. (2005) study was conducted in southern New England, and the Shriver et al. (2007) study was conducted in the same marshes as our investigation. Together, this suggests that the oviposition preferences of sharp-tailed sparrows are similar across both space (~300 km) and time

Table 2 Predictors of female species as measured by summed plumage score in Scarborough, ME, USA (positive beta values correspond to vegetation characteristics with higher values for females toward the saltmarsh sparrow end of the plumage gradient) for vegetation characteristics chosen in the top model

Predictor variable	<i>b</i>	SE	<i>T</i>	<i>P</i> value
Year	-3.20	1.82	-1.75	0.08
Distance from bottom of the nest to the ground (cm)	0.90	0.23	3.84	<0.001
Nest depth (cm)	-1.35	0.55	-2.44	0.02
Thatch depth at center (cm)	0.44	0.17	2.61	0.01
Thatch depth at 1-m ² quadrat midpoints (cm)	-0.35	0.26	-1.36	0.18
Maximum vegetation height at 1-m ² quadrat midpoints (cm)	-0.18	0.10	-1.69	0.09
Average vegetation height at center (cm)	-0.36	0.12	-2.95	<0.01
<i>Spartina patens</i> (% cover)	-0.18	0.04	-4.79	<0.001
<i>Distichlis spicata</i> (% cover)	-0.18	0.04	-4.02	<0.001
<i>Juncus gerardii</i> (% cover)	-0.13	0.09	-1.50	0.14

Table 3 Predictors of daily nest survival probability in Scarborough, ME, USA for vegetation characteristics chosen in the top model

Predictor variable	<i>b</i>	SE
Year	0.67	0.33
Distance from bottom of the nest to the ground (cm)	-0.07	0.04
Nest depth (cm)	-0.12	0.11
Thatch depth at center (cm)	-0.03	0.03
Thatch depth at 1-m ² quadrat midpoints (cm)	0.05	0.05
Maximum vegetation height at 1-m ² quadrat midpoints (cm)	-0.01	0.02
Average vegetation height at center (cm)	0.03	0.02
<i>Spartina patens</i> (% cover)	0.01	0.01
<i>Distichlis spicata</i> (% cover)	-0.004	0.01
<i>Juncus gerardii</i> (% cover)	0.002	0.01

(~a decade). Additionally, we found that compared to randomly selected points, the 1-m² plot surrounding nest sites included less water, a trait that was not examined by the two previous studies.

Saltmarsh and Nelson's sparrow females exhibit consistently different oviposition preferences as measured by vegetation characteristics. For example, females with plumage more typical of saltmarsh sparrows built nests that were higher above the ground, had shallower nest bowls, and placed them in areas with less *Spartina patens* compared to females that exhibited plumage more typical of Nelson's sparrows. Because these species interbreed in sympatry, the observed differences in oviposition preferences between them in this population are conservative underestimates for the species in general because some degree of convergence is expected from genetic introgression.

The nest characteristics that differed by species did not predict either of two estimates of fecundity, however. Though the oviposition preferences of saltmarsh and Nelson's sparrows vary consistently across study sites, they do not appear to confer any adaptive advantage in terms of fecundity as measured by nest survival or brood size during the years of our study. In fact, the nest traits that together explain 33 % of the observed variance in female species perform worse at predicting nest survival than an intercept-only null model. Our findings are consistent with previous research, which has found no placement differences between successful and unsuccessful nests (Gjerdrum et al. 2005; Shriver et al. 2007). Furthermore, we found no evidence that saltmarsh and Nelson's sparrows exhibit differences in two life history traits that could result in patterns of fecundity that differ from those observed in nest survival probabilities (renewing rate and clutch size). Thus, nest survival is likely a reasonable index of the fitness consequences of oviposition divergence in this system and a better index than has been reported in other songbirds (Streby and Andersen 2013; Streby et al. 2014).

Here, we show direct evidence that two estimates of fecundity are not related to divergent oviposition preferences of saltmarsh and Nelson's sparrows. However, oviposition preference can maximize fitness in a number of other ways. Refsnider and Janzen (2010) review nest survival (more generally, embryo survival) in addition to five alternative hypotheses for how oviposition site can maximize fecundity. Sharp-tailed sparrows provide an ideal system that offers good reason to eliminate the alternative hypotheses, however, suggesting that the divergent oviposition preferences between saltmarsh and Nelson's sparrows are currently non-adaptive.

We can rule out four of Refsnider and Janzen's (2010) hypotheses because of the unique mating systems and life histories of saltmarsh and Nelson's sparrows. First, Refsnider and Janzen describe a hypothesis that oviposition site can indirectly maximize fitness through mate choice, but both saltmarsh and Nelson's sparrows are promiscuous and non-territorial, and males do not contribute to parental care (Greenlaw and Rising 1994; Shriver et al. 2010). Second, the authors propose that oviposition site can impact fitness through offspring phenotype, usually via microclimatic conditions. This hypothesis is commonly invoked for species that do not exhibit parental care, such as fish, amphibians, and reptiles. In most bird species, including sharp-tailed sparrows, adults mediate the environmental conditions at the oviposition site through incubation and nest attendance. Nonetheless, this idea has been applied to several avian systems, providing mixed results as to whether differences in nest microclimates are typically ameliorated by parental behavior (Rauter et al. 2002; Amat and Masero 2004; Dawson et al. 2005; Robertson 2009; Tieleman et al. 2014). Sharp-tailed sparrow females nest under natural or woven grass canopies, which create shade and moderate the nest microclimate. Thus, we think microclimate is unlikely to affect offspring phenotype in this system, but future studies should measure microclimatic conditions at the nest site to address this possibility. Third, oviposition site can also maximize fitness via juvenile survival, for example

by proximity to suitable habitat for juveniles after leaving the nest. Sharp-tailed sparrow juveniles roam the marsh after leaving the nest, however, in home ranges that overlap with non-parental adults and parental adults, conspecifics, and heterospecifics (Shriver et al. 2010; KJR unpublished data). Therefore, juvenile habitat use and any consequent differences in juvenile survival are not likely to result from any differences in oviposition preference between the species. Instead, juveniles of both of these non-territorial species are exposed to similar post-fledging risks to survival that are independent of oviposition site. Fourth, oviposition preference is hypothesized to maximize fitness by maintaining natal philopatry in some systems. Both saltmarsh and Nelson's sparrows exhibit natal philopatry, but on the larger spatial scale of marsh habitat patches, which is on the order of hectares rather than within 1-m² plots that were examined in this study (Greenlaw and Rising 1994; DiQuinzio et al. 2001; KJR unpublished data).

The fifth and final alternative hypothesis described by Refsnider and Janzen (2010) is that oviposition site can maximize fitness via female survival. We cannot conduct a survival analysis with only 2 years of data, and we observed too few females that nested in both years of this study to make any inferences about female survival based on species (two within the saltmarsh sparrow plumage limit, one Nelson's sparrow, and two apparent hybrids). However, we also conducted systematic mist-netting at these study sites for another project, and we detected similar proportions of saltmarsh and Nelson's sparrow females captured in 2012 that returned in 2013 (8.7 % of Nelson's sparrow females, 5.5 % of saltmarsh sparrow females; KJR unpublished data). Additionally, adult survival estimates calculated from systematic mist-netting at these and additional sites demonstrated that saltmarsh and Nelson's sparrow females exhibit equivalent adult survival rates across northern New England (CR Field unpublished data). Moreover, Sillett and Holmes (2002) observed that monthly rates of mortality were 15 times greater during migration months than in the breeding season for another songbird species. While oviposition site may influence female survival in sharp-tailed sparrows, in these and many songbirds, adult mortality related to oviposition site is likely small relative to migration-related mortality. Nonetheless, future studies should include explicit tests for female survival and more robust estimates of fecundity that include juvenile survival.

Despite the limitations of our study, our findings are consistent with the hypothesis that neutral processes have shaped or currently maintain species-level differences in oviposition preference. The two sharp-tailed sparrow species in Scarborough Marsh share evolutionary history, sympatric habitat, a unique mating system, and developmental constraints, and thus we can reject many mechanisms for adaptive divergence. We are left with drift as a likely driver of the maintenance of the observed divergence between saltmarsh and Nelson's sparrow oviposition preferences. The possibility

that either species currently exhibits an oviposition preference that arose through adaptive selection elsewhere in space or time is impossible to eliminate. At the very least, we can conclude that the current divergence in saltmarsh and Nelson's sparrow oviposition preferences is maintained without strong selection in sympatry. Should these traits become important for reproductive isolation between the species in the future, that outcome will have been shaped at least partly by periods of neutral evolution.

These results challenge the often-assumed paradigm that traits, particularly those related to survival, fecundity, and reproductive isolation, are optimized. In light of these and other similar findings, researchers should explicitly measure the fecundity consequences of variation in oviposition preferences. In particular, wildlife managers should consider that observed preferences and behaviors in wildlife are not necessarily adaptive when planning for conservation action such as habitat restoration. Otherwise, they may take conservation action that, while based on observed habitat use, will not result in increased population growth.

Our results suggest that, as with all traits, oviposition preference can vary neutrally and is perhaps a work in progress. Oviposition preference is not perfectly optimized to the environment, nor is it without superfluity. This standing variation in oviposition preference, which exists not just at the individual but at the population level, provides fodder for divergence and ultimately could increase the probability of ecological speciation. More research should address how common neutral variation in oviposition preferences is in nature, and its relative importance in the speciation process.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (Institutional Animal Care and Use Committee of the University of Maine under approval A2011-04-02).

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