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Local density regulates migratory songbird reproductive success through effects on double-brooding and nest predation

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Abstract. Knowledge of the density-dependent processes that regulate animal populations is key to understanding, predicting, and conserving populations. In migratory birds, density-dependence is most often studied during the breeding season, yet we still lack a robust understanding of the reproductive traits through which density influences individual reproductive success. We used 27-yr of detailed, individual-level productivity data from an island-breeding population of Savannah sparrows *Passerculus sandwichensis* to evaluate effects of local and total annual population density on female reproductive success. Local density (number of neighbors within 50 m of a female's nest) had stronger effects on the number of young fledged than did total annual population density. Females nesting in areas of high local density were more likely to suffer nest predation and less likely to initiate and fledge a second clutch, which led to fewer young fledged in a season. Fledging fewer young subsequently decreased the likelihood of a female recruiting offspring into the breeding population in a subsequent year. Collectively, these results provide insight into the scale and reproductive mechanisms mediating density-dependent reproductive success and fitness in songbirds.

Key words: density-dependence; fecundity; fitness; path analysis; population regulation; recruitment; Savannah sparrow; structural equation model.

Introduction

Knowledge of the processes that limit and regulate animal populations is key to understanding past population change and for predicting, managing, and conserving populations in the future (Lack 1954, Hixon et al. 2002, Faaborg et al. 2010). Population regulation occurs through density-dependence, which is the negative relationship between a population's growth rate, underlying vital rates, and size (Sibly et al. 2005). Many studies have sought to detect as well as quantify the strength and shape of density-dependence in wildlife populations, primarily using time-series of population counts, productivity, and mark-recapture data (Coulson 2001, Gill et al. 2001, Koons et al. 2015, Sæther et al. 2016). However, density-dependence at the population level is ultimately the accumulation of density effects on components of individual fitness. How, and at what scale, density influences individual reproductive success, condition, and survival is not well understood.

Resource competition is the primary mechanism by which density-dependence regulates populations (Lack 1954, Newton 1998). As populations grow, so does competition for resources such as space and food. Crowding can lead to increased time and energy spent competing with conspecifics to defend territories (Rodenhouse et al. 2003, Sillett et al. 2004), thereby reducing time and energy available for self-maintenance and reproduction. Crowding can also modify interspecific competition, predator-prey interactions (Arcese et al. 1992, Gunnarsson and Elmberg 2008), and transmission of parasites and disease (Hochachka and Dhondt 2000). In heterogenous habitats, crowding effects can be magnified by site-dependent regulation, where population growth forces more and more individuals into poorer habitat where survival and reproduction are more challenging (Ferrer and Donazar 1996, Rodenhouse et al. 1997, 2003, Nevoux et al. 2010). Taken together, these are all potential means by which density can influence individual reproductive success, condition, and survival, and ultimately serve to regulate population vital rates and growth.

In migratory songbirds, density-dependence has primarily been studied during the breeding season, yet we still lack a robust understanding of the specific reproductive traits that mediate density-dependent fecundity (Arcese et al. 1992, Rodenhouse et al. 2003, Sillett et al. 2004). Even less clear is the extent to which density-dependent effects on reproductive success can carry forward to influence recruitment of individuals into the breeding population. The amount that a given reproductive attempt contributes to an individual's fitness depends first on the number of offspring produced and then whether those offspring survive and recruit into the breeding population. Thus, effects of density on reproductive success and recruitment not only contributes to population regulation but can also influence individual fitness. To fill these two knowledge gaps, we need

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detailed individual-level breeding and recruitment data under varying population densities.

In a recent study, we found evidence for density-dependent regulation of per-capita female fecundity and first-year survival in a migratory songbird, the Savannah sparrow *Passerculus sandwichensis* (Woodworth et al. 2017). Here, we used 27-yr of detailed, individual-level reproductive data from the same breeding population on Kent Island in the Bay of Fundy, New Brunswick, Canada to evaluate (1) the reproductive traits through which density affects female reproductive success, (2) the spatiotemporal scale at which density-dependent effects are greatest, and (3) the potential for density to influence female fitness through offspring recruitment. To achieve these objectives, we used path analysis (Shipley 2009) to first quantify direct effects of four reproductive traits (timing of breeding, clutch size, nest predation, and double-brooding) on variation in the number of young fledged and then estimate direct effects of density at two spatiotemporal scales on the four reproductive traits. The two scales we considered were "local", which corresponded to the number of neighboring pairs within 50-m of a female's nest(s), and "annual", which corresponded to the total population size in each year. We then generated predictions of the number of young fledged and offspring recruited under different simulated densities to compare the relative effects of density at the two spatiotemporal scales on variation in young fledged and probability of recruiting offspring.

The four reproductive traits we considered, clutch size (Arcese et al. 1992), timing of breeding (Norris et al. 2004), nest predation (Sherry et al. 2015), and double-brooding (Nagy et al. 2005, Townsend et al. 2013, Hoffmann et al. 2015), are known to influence individual reproductive success and, thus, represent routes through which density-dependent productivity could arise. Under a crowding mechanism, time and energy spent defending territories is expected to delay breeding or limit energy available to allocate to egg production (Arcese et al. 1992). Crowding can also affect nest predation rates, either by attracting or repelling predators (Schmidt and Whelan 1999, Giroux et al. 2016). Lastly, the propensity to initiate a second clutch and the success thereof could be directly reduced at high densities if there are insufficient food resources for raising additional young or indirectly through effects on the timing of breeding or higher predation rates (see Appendix S1: Fig. S1 for predicted effects linked to these hypotheses).

Methods

Study system and field methods

Savannah sparrows are ground-nesting, migratory songbirds that breed in grasslands and other open habitats across Canada and the northern USA and overwinter in the southern USA, Mexico, and parts of Central America (Wheelwright and Rising 2008). The population we studied breeds in a ~10-ha study area on Kent Island, NB, Canada (44.48° N, 66.79° W; Fig. 1) and overwinters at the eastern edge of the species-wide winter range, in the southeastern USA (Woodworth et al. 2016). Previous research showing strong density-dependent effects on fecundity and first-year survival (Woodworth et al. 2017), coupled with detailed individual-level productivity data and high natal philopatry (nestling return rate = 11.2%; Wheelwright and Mauck 1998), make this an ideal population in which to study the mechanisms of density-dependent female reproductive success and fitness.

The breeding biology of Savannah sparrows on Kent Island has been studied since the 1960's (Dixon 1978) and has been monitored annually since 1987 (excluding 2005–2007). Each year, population monitoring occurs between late May and the end of July and involves capturing and color-banding new members of the population, re-sighting returning color-banded individuals, mapping breeding territories, finding and monitoring nests, and banding nestlings. All individuals in the breeding population are marked with a United States Fish & Wildlife Service or Canadian Wildlife Service (USFWS/CWS) aluminum leg-band and a unique combination of three plastic color leg-bands. Nestlings born in the study population are banded in the nest 7 d after hatching with a USFWS/CWS aluminum leg-band and one color leg-band. Nestlings that return to the study population in a subsequent year (local recruits) are recaptured, identified, and given a complete three-color leg-band combination.

Breeding territories are determined from daily observations of the behaviors and movements of individuals (e.g., locations of singing males and nests). Savannah sparrows on Kent Island typically form socially monogamous breeding pairs, but a variable fraction of males (15–43%) will pair with more than one female (Wheelwright et al. 1992). Although female mating behaviour has the potential to influence their reproductive success, Wheelwright et al. (1992) found that female Savannah sparrows on Kent Island that were mated to a polygynous male had similar reproductive success to females that were monogamously-mated. This finding is supported by data from the most recent 22-yr of the long-term study. From 1987 to 2016, the mean (±SE) number of young fledged was 4.3 ± 0.1 for monogamous females compared to 4.2 ± 0.1 for females mated to a polygynous male. As such, we excluded mating status from subsequent analyses of factors influencing female reproductive success.

Nests are typically found at the beginning of incubation and are checked every second day to determine dates of hatching and fledging or failure, numbers of young hatched and fledged, and fate of the nest (fledged, abandoned, or depredated). Savannah sparrows on Kent Island can fledge young from up to two clutches in a single season (known as "double-brooding"). Hereafter, we refer to the two clutches of a double-brooded female as the "first clutch" and "second clutch". If a female's first clutch is depredated or abandoned, she may re-nest up to

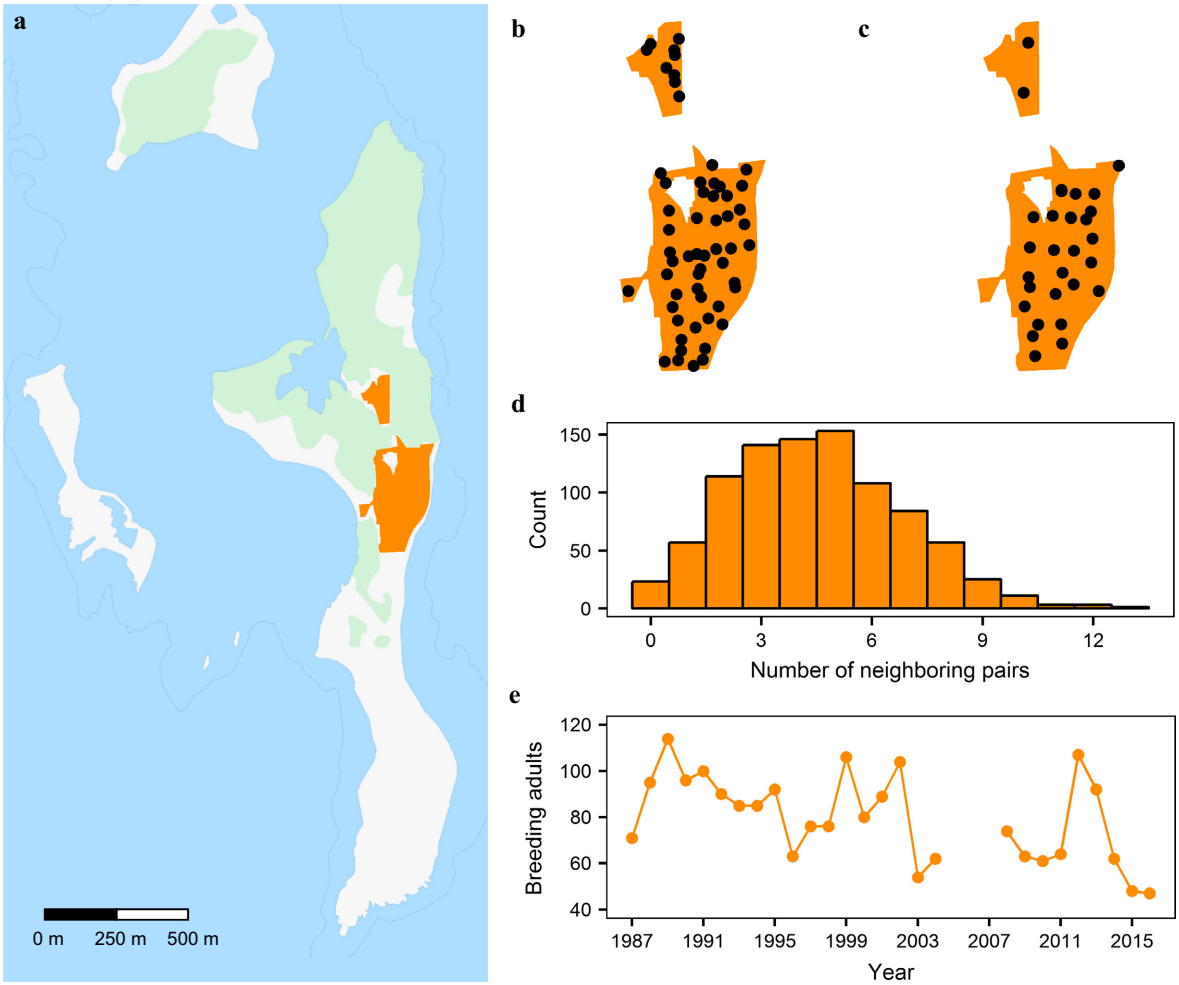

FIG. 1. (a) Map of the long-term Savannah sparrow study area (orange) on Kent Island and the distribution of breeding pairs (black dots) in a year of (b) high population density (2012) and (c) low population density (2015). Points in (b) and (c) represent the average nest location of each breeding pair. (d) Distribution of local densities, as measured by the average number of neighboring pairs within 50-m of a females' nest(s) in a single breeding season, over the 27-yr study period. (e) Variation in the size of the breeding population between 1987 and 2016. The map in (a) was generated using data from OpenStreetMap (www.openstreetmap.org).

three or four times ("replacement clutches"). A "second clutch" refers to the clutch laid by a female after she has successfully fledged young from a first clutch or replacement thereof. Incubation begins once the female has laid her penultimate egg and lasts an average of 12 d, with nestlings remaining in the nest for 9–11 d (Dixon 1978). Both sexes provision young whereas only females build nests and incubate (Wheelwright and Rising 2008). Once each nest has fledged or failed, we recorded its spatial coordinates using a Global Positioning System.

Definitions of reproductive success, traits, and fitness

Reproductive success.—Reproductive success was defined as the total number of young a female fledged in a year. Fledging success of each nest was confirmed on the ninth day after hatching by observing adults bringing food to the nest vicinity. The number of young fledged from a nest was recorded as the number of nestlings banded on the seventh day after hatching. In our analyses, we excluded data for females for which we lacked a complete breeding history (e.g., females for whom we were missing one or more nesting attempts or for which one or more nests was outside the standard study area) or whose nests were the subject of experimental manipulations (e.g., clutch size manipulations; Mitchell et al. 2011, Pakkala et al. 2015).

Timing of breeding.—Timing of breeding was the estimated Julian date on which a female laid her first egg. For females that successfully fledged their first clutch, first egg date was calculated by subtracting 12 d (the average duration of incubation; Dixon 1978) from the hatch date, plus one additional day for each egg laid up

to the penultimate egg. To determine first egg date for females whose initial nest attempt failed, we used data from all nests with known hatch dates to calculate the average difference (in days) between when a nest was found and when it hatched. We then subtracted the difference between this value and the length of incubation period from the found date of each failed nest. Lastly, as with nests that successfully hatched, we then subtracted 1 d for each egg laid up to the penultimate egg.

Clutch size.—Clutch size was defined as the average number of eggs laid across all first clutches (first attempt and any replacement clutches) of a female in a given year. The average (±SE) size of first clutches and replacements thereof was 4.2 ± 0.02 eggs over the course of the study period, compared to 3.8 ± 0.04 eggs for second clutches.

Nest predation.—For our analyses, we categorized females as either having suffered nest predation or not. On average, 24% of nests are depredated in a breeding season, but the proportion varied among years (range = 6–54%). The most likely nest predator of Savannah sparrow nests on Kent Island is the American crow *Corvus brachyrhynchos* (Wheelwright et al. 1997). This species breeds on the island, often in trees on the perimeter of the study area, and is frequently observed foraging on the ground where Savannah sparrows nest. Only two other avian nest predators have been consistently observed on the island since the start of the long-term Savannah sparrow study. The Common raven *Corvus corax* breeds on Kent Island but is far less abundant than the American crow (N. T. Wheelwright and D. R. Norris, *personal observation*) and a breeding colony of Herring gulls *Larus argentatus* overlaps with approximately one quarter of the southern Savannah sparrow study field. However, although gulls opportunistically depredate Savannah sparrow eggs or nestlings that they encounter, nest predation inside the gull colony tends to be lower than outside of the colony, likely because gulls aggressively defend their own nests against crows (Wheelwright et al. 1997). No mammalian predators exist on Kent Island.

Double-brooding.—For our analyses, we defined females as either having successfully fledged a second clutch or not. Over the 27-yr study, on average, 29% of all females attempted a second clutch in a given year (range = 14–58%). Among the females that were successful on their first nest attempt, 56% attempted a second clutch (range = 20–92%). In an average year, 90% of second clutches were successful (range = 63–100%), whereas only 67% of first clutches were successful (range = 35–92%).

Recruitment.—To evaluate potential effects of density on female fitness as mediated by their reproductive success the previous year, we determined whether the offspring produced by a female recruited into the breeding population in a subsequent year. Between 1987 and 2015, the average (apparent) first-year survival probability was 10.1% (range = 4.4–18.5%; Woodworth et al. 2017). We excluded juveniles born in 2004 from our recruitment analyses because population monitoring was interrupted from 2005–2007 and recruitment was unknown. Juveniles born in 2016 were also excluded because their recruitment is not yet known.

Population density estimates

We evaluated population densities at two spatiotemporal scales: annual and local. Annual density corresponded to the peak number of breeding adults of both sexes in the study area in each year (Fig. 1e). Because unpaired individuals are rare in this population, annual density is equivalent to the total population size. Local density corresponded to the average number of breeding pairs within 50-m of a female's nest(s) (Fig. 1d). Local densities for each female were calculated by placing a 50-m buffer around the spatial coordinates of each of her nests. For each nest, we then extracted all other nests not belonging to the focal female that fell within the 50-m buffer and counted the number of distinct breeding pairs to which the other nest(s) belonged. Since most females attempt more than one nest in a breeding season, we averaged the number of neighboring pairs across nests to produce a single local density estimate for each female in each year.

Consistent with the species-wide population trend (Sauer et al. 2017), Savannah sparrows have been declining on Kent Island since the early 2000's (Woodworth et al. 2017). Prior to 2016, per capita female fecundity was also declining on Kent Island (Woodworth et al. 2017). Therefore, for our statistical analyses, we removed the temporal trend in population density ("de-trended"; Graham 2003) to avoid spurious detection of density-dependence due the co-occurrence of a temporal decline in population size and fecundity (Grosbois et al. 2008).

Statistical analysis

We evaluated the scale and reproductive mechanisms mediating density-dependence of female reproductive success using a mixed-effects path modelling approach (Shipley 2000, 2009). We fitted two path models, one for local density and the other for annual density, each of which consisted of six sub-models. The first sub-model related the probability of a female recruiting one or more offspring into the breeding population in year t to the number of young she fledged in year $t-1$ and density (local or annual) in year $t-1$. The second sub-model related the number of young fledged by a female to the four reproductive traits and density. The final four sub-models related the reproductive traits to density. The sub-models for clutch size, predation, and double-brooding also included a fixed effect for timing of breeding. The sub-model for double-brooding also included a

fixed effect for predation (see Appendix S1: Fig. S1 for a graphical representation of the full path models).

Sub-models were fitted using generalized-linear mixed-effects models implemented in the R package *lme4* (Bates et al. 2015). Recruitment probability, double-brooding, and predation were modeled with a binomial distribution (logit link), whereas the number of young fledged was modeled with a Poisson distribution (log link). Clutch size and timing of breeding were standardized in all analyses and modeled with a Gaussian distribution (identity link). All sub-models included year as a random effect to account for among-year differences in environmental conditions, that could have influenced productivity, as well as a random effect for individual ID to account for repeated measures of the same female. Finally, all sub-models included a fixed effect for female age to account for age-related differences in reproductive performance between first time breeders and individuals that had bred in the study population in at least one previous year (Wheelwright and Schultz 1994).

To compare total effects of density at the two spatiotemporal scales on young fledged and recruitment, we first derived the most parsimonious path model for local and annual density using an AIC model selection procedure (Shipley 2013, model selection description and results are available in Appendix S1: Supplementary Method S1 and Appendix S1: Tables S1–S4). We then used the best model for each spatiotemporal scale to predict the number of young fledged and probability of recruitment under simulated changes in density. For both local and annual density, we restricted simulated densities within the range of observed densities. For local density (de-trended number of neighboring pairs; range = −5.7 to 7.3, SD = 2.2), we predicted number of young fledged and recruitment when we added −4, −2, 0, +2, +4, and +6 pairs to the de-trended local density experienced by each female in each year. For annual density (de-trended number of breeding adults; range = −24.3 to 38.5, SD = 16.1), we predicted the number of young fledged and recruitment when we added −20, −10, 0, +10, +20, and +30 breeding adults to the de-trended annual density experienced by each female in each year. We simulated 1,000 predictions of young fledged and recruitment probability for each change in density. In each simulation, predicted values for binomial responses (predation, double-brooding, recruitment) were drawn from a binomial distribution where the input probabilities were those predicted by the respective sub-models. Predicted numbers of young fledged and recruitment probabilities were then summarized across simulations for each change in density (Fig. 3).

All statistical analyses and spatial operations for determining local densities were performed in R (R Core Team 2016). R code for generating model predictions for young fledged and offspring recruitment probability under simulated changes in local and annual density are provided in Data S1. Figures were produced using the R package ggplot2 (Wickham 2009).

Results

We quantified the reproductive success of 534 females that collectively comprised 1,567 nest attempts over the course of the 27-yr study period. Over half (57%) of the females bred in only 1 yr of the study, but four individuals bred for 6 yr and another for 7 yr. The average (±SE) number of young fledged per female per season was 4.2 ± 0.1 (range = 0–10). Of the 3,692 young fledged over the course of the study (excluding 2004 and 2016), 10% (n = 380) recruited into the breeding population the subsequent year. Over half (57%) of the females failed to recruit a single offspring into the population over their lifetime, whereas 26% recruited one offspring and 17% recruited two or more offspring (maximum = 9).

Contributions of reproductive traits and age to reproductive success

All four reproductive traits were retained in the final path models for both local and annual density (Fig. 2). Females that produced larger clutches (β ± SE = 0.12 ± 0.02) and that fledged young from two clutches in a season (β ± SE = 0.58 ± 0.04) produced more offspring than females that laid fewer eggs and fledged only one clutch in a season (Fig. 2). Double-brooded females produced an average (± SE) of 7.0 ± 0.1 fledglings compared to only 3.3 ± 0.1 offspring produced by single-brooded females (β ± SE = 0.58 ± 0.04). As expected, nest predation (β ± SE = −0.30 ± 0.04) and timing of breeding (β ± SE = −0.06 ± 0.03) both had negative effects on the number of young fledged (Fig. 2). Among females that did not attempt a second clutch, those that did not experience nest predation produced 3.6 ± 0.1 offspring per year compared to 2.8 ± 0.1 offspring produced by those that lost one or more nests to predators. Females that laid their first egg after the mean first egg date (31 May or mean [±SD] Julian date = 152 ± 7 d) averaged 1.4 fewer young fledged compared to those that initiated egg-laying on or before the mean first egg date.

Female age was also retained in the final path models and influenced female reproductive success both directly and indirectly through the reproductive traits (Wheelwright and Schultz 1994). Experienced breeders (those that bred in the population in at least one previous year) tended to produce more offspring than first-time breeders (β ± SE = 0.06 ± 0.03). Furthermore, experienced females also bred earlier, laid larger clutches, were more likely to initiate and fledge a second clutch, and were less likely to lose a nest to predation compared to first-time breeders (Fig. 2).

Direct effects of density on reproductive traits and success

Both local and annual density influenced female reproductive success but, despite being strongly correlated (Pearson's r for annual density vs. mean local density = 0.74), their effects differed in strength and were

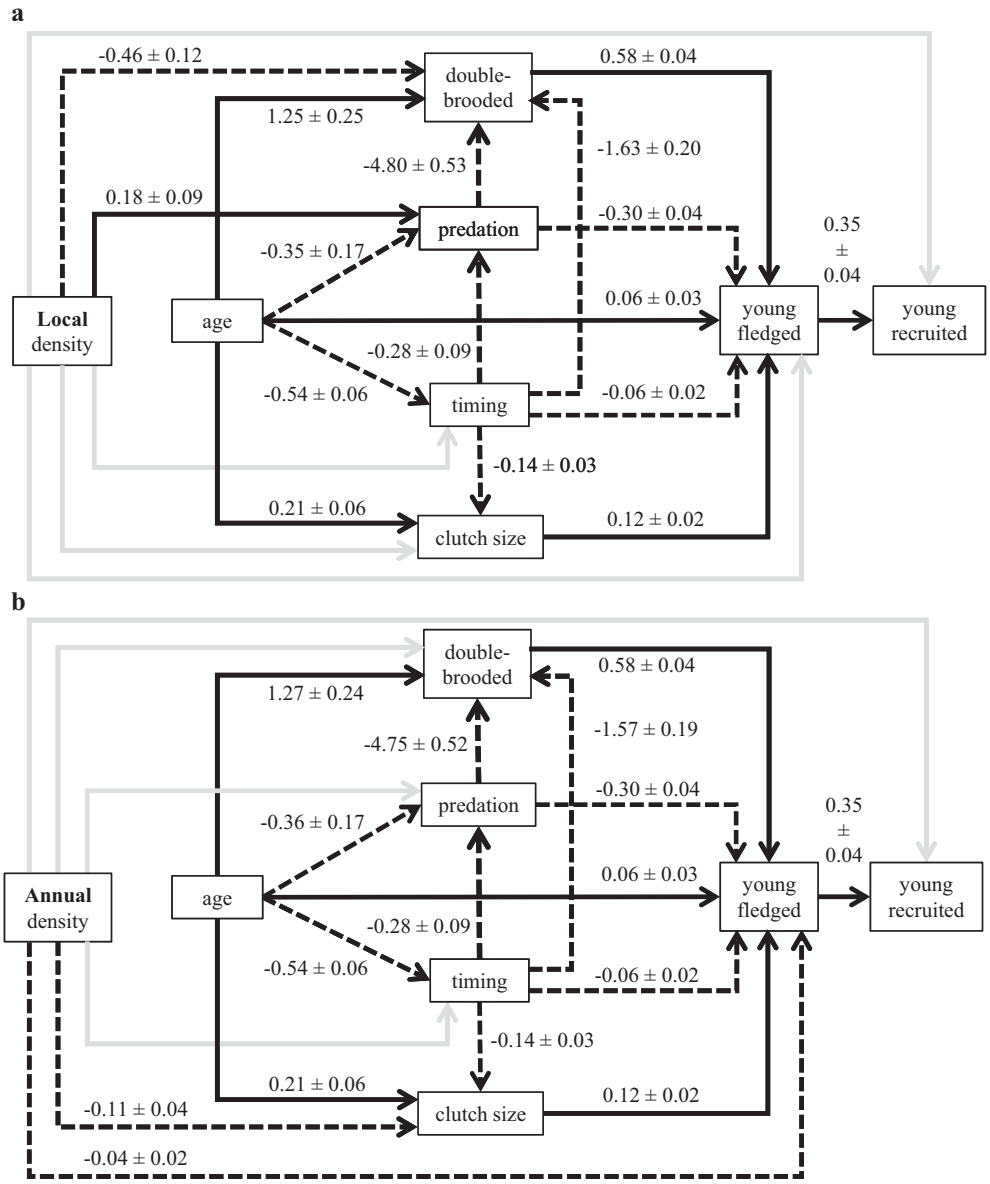

FIG. 2. Final path models following AIC model selection showing direct and indirect effects of density at two spatiotemporal scales, (a) local and (b) annual, on female reproductive success and offspring recruitment. Black lines represent paths included in the final model and grey lines show paths excluded from the final model. Solid lines show positive effects and dashed lines show negative effects. The values associated with each path correspond to slope estimates (±SE) from the sub-models (see Appendix S1: Tables S1–S4 for the model selection results).

mediated by different reproductive traits (Fig. 2). Local density had a strong negative effect on double-brooding and a positive effect on nest predation, such that females that nested in areas of high local density were more likely to suffer nest predation and less likely to fledge a second clutch (Fig. 2a). Double-brooding was also strongly negatively influenced by nest predation and, thus, was affected by density both directly as well as indirectly through nest predation (Fig. 2a). After accounting for variation explained by the reproductive traits, local density did not have a direct effect on female reproductive success (Fig. 2a). In contrast, annual density had a direct negative effect on young fledged, as well as an indirect effect on young fledged through clutch size (Fig. 2b). Annual density did not influence nest predation or the probability of initiating and fledging young from a second clutch.

Timing of breeding was the only reproductive trait that was not influenced by local or annual density (Fig. 2a, b). However, timing of breeding did influence clutch size, double-brooding, and nest predation. Females that bred earlier tended to lay more eggs and

were more likely to initiate and fledge young from a second clutch, but they were also more likely to suffer nest predation (Fig. 2a, b).

Cumulative effects of local and annual density on reproductive success and recruitment

Overall, female reproductive success was influenced more strongly by local than by annual density (Fig. 3). Predicted reproductive success declined by 0.91 offspring per female (from a mean of 4.65 to 3.74 fledglings per female) over the range of simulated local densities. In contrast, predicted reproductive success declined by 0.53 offspring per female (from a mean of 4.45 to 3.92 fledglings per female) over the range of simulated annual densities. In turn, the probability of recruiting an offspring into the study population was also more strongly influenced by local compared to annual density (Fig. 3b, d). Predicted recruitment probability declined by 6.9% in response to changes in local density compared to 3.8% in response to changes in annual density.

Discussion

Our study elucidates the reproductive traits that mediate density-dependent reproductive success and the scale at which density influences these traits. We found that female reproductive success was primarily regulated by local density through effects on nest predation and double-brooding. As density increased, females were more likely to suffer nest predation and less likely to initiate and fledge young from a second clutch, thereby lowering their reproductive success. Importantly, we also show that density-dependent regulation of reproductive success can carry forward to influence recruitment of offspring into the breeding population. At high densities, females fledged fewer young which, in turn, reduced their probability of recruiting offspring.

Although density-dependent effects on reproductive traits have been detected at a population-level for several songbird species (Müller et al. 2004, McKellar et al. 2013*a*, Gullett et al. 2015) and many studies have related variation in reproductive success to different reproductive

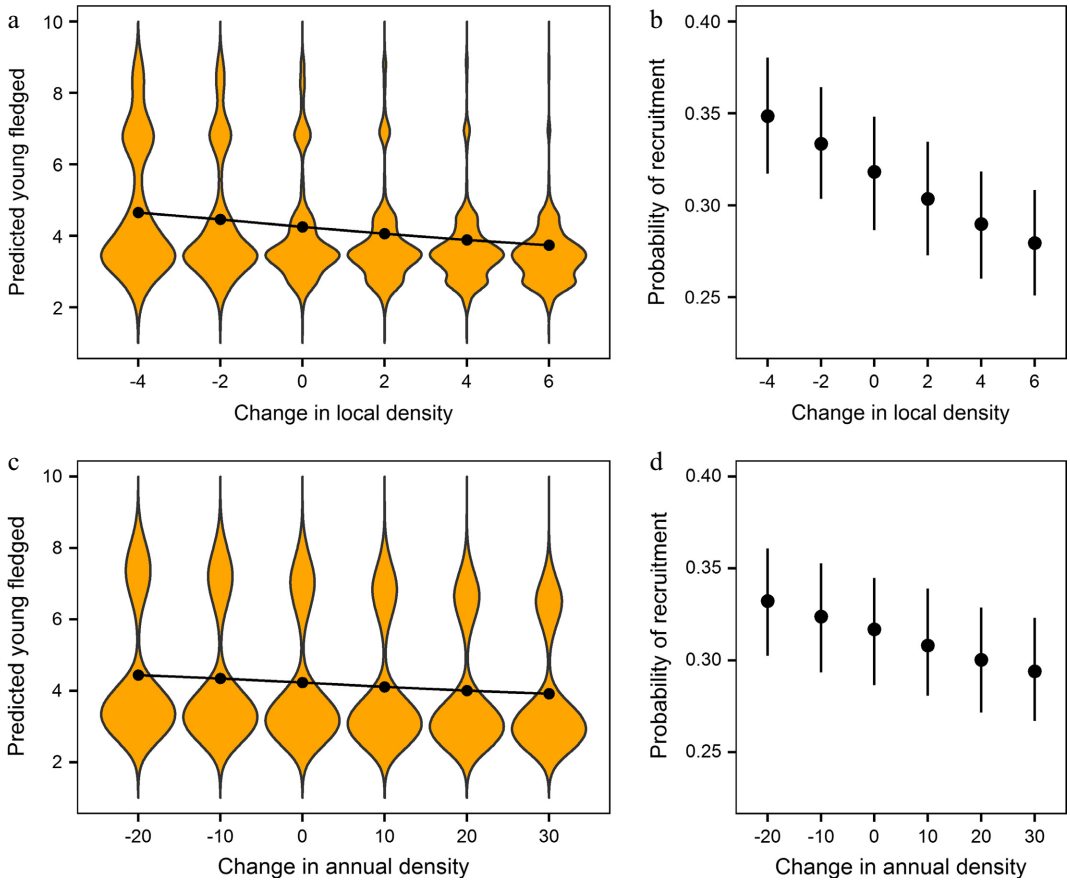

Fig. 3. Predicted effects of variation in local and annual density on female (a, c) reproductive success and (b, d) offspring recruitment as mediated by the reproductive traits. Predicted changes in reproductive success are shown using violin plots, where the shape and length of the violin is based on kernel density estimation of the distribution of young fledged (Hintze and Nelson 1998). Offspring recruitment probabilities for each change in density were averaged across females, with error bars showing the upper and lower 95% quantiles. Predictions were generated from the final path models shown in Fig. 2.

traits (Verhulst et al. 1995, Müller et al. 2004, McKellar et al. 2013*b*, Hoffmann et al. 2015), rarely are the two parts quantitatively linked to investigate the reproductive processes that mediate density-dependent reproductive success. Path analysis is a useful technique to provide insight into causal mechanisms mediating density-dependent relationships from historic datasets. The ability to infer causal relationships from existing observational data also provides an alternative to experimental manipulations of density, which can pose ethical challenges and may not be a viable option for many species, avian or otherwise (e.g., species-at-risk), given that they often require removal or translocation of individuals from a population (Rodenhouse et al. 2003, Sillett et al. 2004, but see Both 1998). In circumstances where manipulations of density are possible, our results provide guidance on the spatiotemporal scale at which density should be manipulated and the types of reproductive traits that may be affected.

Despite being positively correlated, effects of local and annual density on reproductive success varied in strength and were mediated by different reproductive traits. Double-brooding and predation were strongly influenced by local density, but not annual density, whereas the opposite was true for clutch size (Fig. 2). The difference of scale at which density affects double-brooding and clutch size could be related to differences in when females make these reproductive decisions. On average, females laid their first egg of the season on 31 May and thus, the amount of energy available for egg production is determined early in the spring when territory boundaries are still being settled and females are likely competing for limited resources with a greater proportion of the population compared to later in the season. In contrast, second clutches were initiated, on average, a full month later in the season when breeding pairs and territories are well established and, therefore, the decision to double-brood is likely shaped by resource availability and competition in the more immediate environment (Sillett et al. 2004, Nagy et al. 2005). Nest predators with large daily home ranges, such as crows, are also likely to cue into areas of high local densities due to the higher probability of encountering a nest (Roos 2002, McKellar et al. 2013*a*, Giroux et al. 2016).

Timing of breeding had direct effects on reproductive success and each of the reproductive traits, but it was not strongly affected by density at either spatiotemporal scale. The lack of a density effect suggests that timing of breeding is more strongly influenced by timing of arrival at the breeding grounds (Woodworth et al. 2016) and/or factors influencing individual condition during the pre-breeding and/or non-breeding seasons (Bêty et al. 2003, Norris et al. 2004). Consistent with Hoffmann et al. (2015) and Townsend et al. (2013), females that bred earlier were more likely to fledge a second clutch (but see Nagy et al. 2005). This effect is likely due to the shortness of the breeding season relative to the amount of time it takes to complete a clutch, fledge young, and care for them until independence (Wheelwright and Templeton 2003). Across all years of the study, 90% of nests were initiated (first egg laid) within a span of just 44 d and the average length of time between initiating first and second clutches was ~30 d. Females that bred earlier also laid larger clutches. Increased investment in egg production early in the season is likely due to the higher survival probability of young the earlier they are fledged in a season (Hochachka 1990, Bêty et al. 2003, Mitchell et al. 2011). However, early breeding is not entirely free of cost. Nest predation, which had a negative effect on both double-brooding and reproductive success, was also higher earlier in the season. This seasonal decline in nest predation is likely a consequence of vegetation growth providing increased nest cover as the season progresses (Borgmann et al. 2013), as well as the increased availability of alternative food sources (e.g., gull eggs and nestlings) to crows (Roos 2002, Borgmann et al. 2013).

In addition to regulating female reproductive success, our results point to a mechanism by which local density can affect fitness. Through negative effects on young fledged, variation in local density caused a 7% decline in predicted offspring recruitment probability, from 35% to 28%. However, given that most females only bred in the population in one or 2 yr, density likely only plays a minor role in determining the total number of offspring recruited by a female in her lifetime. Rather, whether or not a female is successful in recruiting offspring is likely determined more by factors that influence offspring survival, such as individual quality or condition (Both et al. 1999, Mitchell et al. 2011) and environmental conditions experienced during different phases of the annual cycle (Woodworth et al. 2017). It is also important to acknowledge that some offspring disperse away from their natal grounds (Wheelwright and Mauck 1998), so our ability to assess recruitment and, in turn, female fitness is imperfect. Separating emigration and survival is a much broader issue in population ecology, especially for small motile species, and a resolution hinges on the ongoing development of new tracking technologies and modeling techniques (Klaassen et al. 2014, Schaub and Royle 2014).

In summary, our study provides insight into the reproductive mechanisms that mediate density-dependent female reproductive success and offspring recruitment in a migratory songbird. Given the importance of understanding how density influences population vital rates for both basic and applied purposes in ecology, maximizing the use of existing observational data to characterize species-specific density-dependent relationships is essential. Path analysis (Shipley 2000, Grace 2008) is a useful approach to achieving this goal. Collectively, results of such studies will help contribute to a more general understanding of how density-dependent processes contribute to the population dynamics of both migratory and non-migratory species (Sæther et al. 2016).

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