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-303(2(bstudie)-259.4(pdurng)-259.89the)-280.93(breeing)-252.4(sueaong)-340.8(Wye)-2ilg1(,we

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 corre-

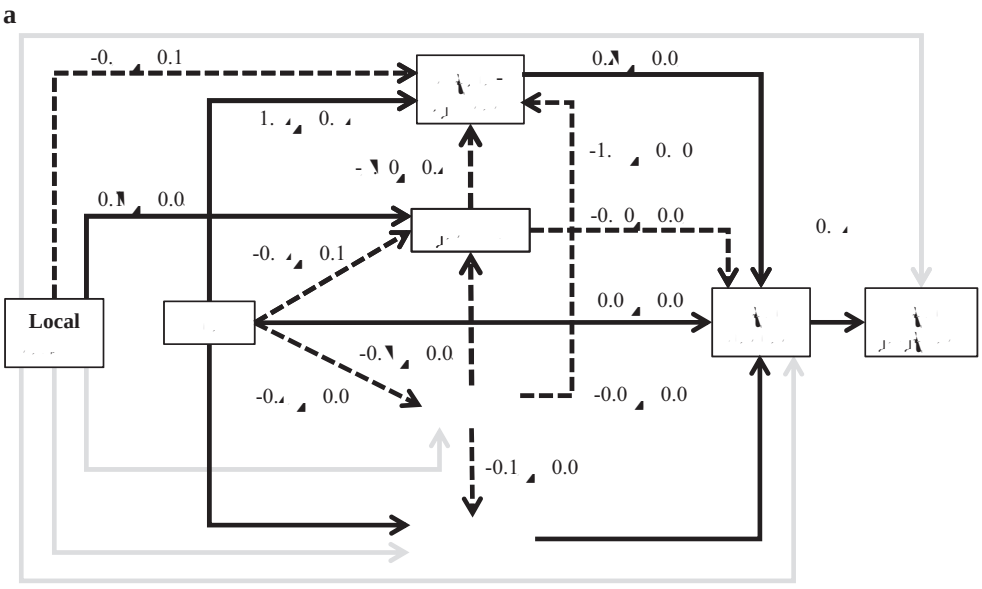
three or four times (“

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

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,



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

traits (Verhulst et al. 1995, Müller et al. 2004, McKellar et al. 2013b, 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. 2013a, Giroux et al. 2016).

Timing of breeding had direct effects on reproductive

sparrow study on Kent Island, especially G. Mitchell and R.