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Neighboring group density is more important than forest stand age to a threatened social woodpecker population

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Effective conservation of group-living forest wildlife requires information on how forest age moderates population parameters. Relationships between forest age and demographics can guide long-term management for wildlife populations that are expanding in relatively young second-growth forests in response to ongoing habitat management. We examined how forest age moderates effects of group density on long-term trends in group size and fledgling production in the endangered red-cockaded woodpecker *Dryobates borealis* (RCW) on the Savannah River Site, SC (SRS). We used 32 years of RCW monitoring data and generalized additive models to: 1) model long-term changes in average RCW group size and fledgling production; and 2) model effects of neighboring group density and neighboring group sizes across a gradient of forest age within 800 m of a group's cavity tree cluster. Average fledgling production oscillated over 2–3 year periods, but longer term evaluation indicated oscillations dampened and average fledgling production slightly decreased over time. Average group size fluctuated abruptly over 2–3 year periods from 1985 to 1994, but longer term evaluation indicated a general increase in group sizes from 1985 to 1994, followed by declines from 1995 to 2007, and a steady increase after 2010. Average fledgling production increased in response to neighboring group density but decreased as neighboring group sizes increased. In contrast, average group sizes increased in response to greater neighboring group density and neighboring group sizes. Stand age did not affect these relationships. Collectively, these results suggest forest age does not directly moderate effects of neighboring group density or group sizes on long-term average group size and fledgling production in the SRS RCW population. Although forest structure has been linked to increased RCW group sizes and productivity, our results suggest that with ongoing habitat management, long-term changes in group size and fledgling production will be driven primarily by group density conditions rather than changing forest age.

Keywords: cooperative breeder, demography, density dependence, population dynamics, red-cockaded woodpecker

Effective conservation of group-living forest wildlife requires information on trends in group sizes and productivity and an understanding of factors influencing these demographic parameters (Newton 1992, Krause and Ruxton 2002). Group density is a main factor driving population trends in group-living wildlife due to its effect on behaviors, group size and productivity (Brown 1969). Long-term increases in group density can lead to a more competitive social environment and declining group productivity trends (Bateman et al. 2012) but may improve demographic connectivity and lead to increasing group size trends (Pépin and Gerard 2008). Consequently, increases in group density over the long-term may result in contrasting group size and productivity trends (Hartmann et al. 2015).

Long-term trends in group size and productivity often cannot be explained by effects of density alone, so additional information on factors that moderate effects of density on group size and productivity may aid management of group-living species. Territory quality moderates effects of density on productivity trends in some group-territorial species because benefits from food resources defended in high-quality territories may offset negative effects of competition at high density (Brouwer et al. 2009). Because high-quality territories tend to support larger groups, increases in territory quality may similarly lead to larger group sizes over time. However, because habitat restoration requires long periods (e.g. forest regeneration after timber harvest; Roberge et al. 2018), anticipated increases in group size and productivity among woodland birds may not occur for decades (Griesser and Lagerberg 2012, Perry et al. 2018). Therefore, after controlling for effects of group density, the relative importance

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of territory quality to group size and productivity trends may be difficult to detect without long-term monitoring data (Holmes and Sherry 2001).

Emerging research suggests moderating effects of territory quality on density-dependent trends in group-living species are not consistent, which could be explained by small-scale processes related to sociality that operate over the long term (Bateman et al. 2013, Cozzi et al. 2018). Among cooperative breeding bird species intense competition for limited breeding vacancies at high density can reduce fitness independent of territory quality (Brouwer et al. 2009). On the other hand, increases in group density can facilitate beneficial social interactions (e.g. prospecting interactions prior to juvenile dispersal; Kesler and Haig 2007, Cox and Kesler 2012) that promote larger group sizes over time (Newton 1998). Positive group-size effects on productivity are so large in many cooperatively breeding birds they can offset negative effects of competition on productivity (Courchamp et al. 1999, Meade et al. 2010), even in low quality habitat (Cusick et al. 2018). This could have important implications for conservation of cooperative breeders with narrow habitat requirements because future declines in productivity may reflect density-dependent competition and small group sizes, rather than habitat degradation (Heuck et al. 2017). Therefore, in addition to long-term data on territory quality, identifying factors moderating effects of density on group size and productivity trends for cooperative breeders requires long-term data at the scale of individual territories where groups interact and compete (Brouwer et al. 2006).

In this study, we examine how forest age moderated effects of group density on long-term trends in group size and productivity in the federally endangered red-cockaded woodpecker *Dryobates borealis* (RCW) (Chesser et al. 2018) on the Savannah River Site, South Carolina (SRS). We used 32 years of demographic data to: 1) model RCW group size and productivity trends; and 2) compare effects of group density conditions on trends across a gradient of territory quality, defined by average stand age. RCWs provide a good case study for investigating differences in long-term group size and productivity trends because they are a group-territorial and cooperatively breeding species that prefers mature open pine forests and requires large and old living pines (e.g. >35 cm dbh and >60 years old) for cavity excavation (Conner and O'Halloran 1987, Conner et al. 2001, U.S. Fish and Wildlife Service (USFWS) 2003). Habitat use and cavity tree selection by RCWs are driven largely by stand age (Jackson and Jackson 1986, DeLotelle et al. 1987, Zwicker and Walters 1999). Increases in stand age are linked to greater group density (Conner et al. 1999), larger group sizes and increased reproductive success (DeLotelle and Epting 1988, Walters et al. 2002a), likely due to greater abundance of large and old pines for cavity excavation (Wahlenberg 1946, Varner and Kush 2004) and increased food availability (Hanula et al. 2000). Foraging RCWs typically select large living pines in stands >60 years old (Zwicker and Walters 1999), but have been observed foraging in stands as young as 30 years (Franzreb 2004).

Anticipating long-term effects of territory quality and group density on trends in fledgling production and group size will gain importance in recovery of RCW populations as they expand into new habitat in younger forest stands receiving ongoing management. Historical RCW populations totaled more than 1.6 million breeding groups, which declined to approximately 3500 groups with <10 000 birds by 1978 (USFWS 2003). RCW populations continued to decline through the 1980s, but increased to more than 5500 group territories and >14 000 birds by the early 2000s (USFWS 2003). Populations across the species' range have remained stable or continued to increase, with range-wide population size recently estimated at more than 7800 group territories (Miller et al. 2019). As a social species, increases in group density that contribute to population recovery result in increasing group size trends over the long-term due to improved demographic connectivity (Engstrom and Mikusinski 1998, Schiegg et al. 2006). Such increases in local group density may lead to crowding that reduces fledgling production (Heppell et al. 1994, Garabedian et al. 2018a), but may increase group sizes by facilitating juvenile dispersal and breeder replacement (Schiegg et al. 2002, Garabedian et al. 2018b). Reduced fledgling production from competition at high density could be offset over the long-term through positive effects of larger group sizes (Conner et al. 2004) or increases in forest age (Reed and Walters 1996, Engstrom and Sanders 1997, Walters et al. 2002a). However, little research has explored relationships between stand age and long-term demographic trends (Garabedian et al. 2014a).

The SRS RCW population has expanded dramatically over several decades of intensive management using artificial nest cavities (Franzreb 1997), although the majority of foraging habitat for individual groups does not satisfy current range-wide structural habitat standards (Garabedian et al. 2014b). Thus, long-term relationships between RCW demographics and forest stand age may provide additional insight into standards of habitat quality. As a group-territorial species that is subject to crowding effects at high group density (Garabedian et al. 2018a), we hypothesized RCW fledgling production would decrease over time, and that increases in group density would have negative effects on fledgling production. Additionally, because stand age and group size have been linked to improved reproductive success (Engstrom and Sanders 1997, James et al. 1997, 2001, Walters et al. 2002a), we hypothesized that increases in forest stand age and group sizes would have positive effects on fledgling production. As a social species with limited dispersal (Pasinelli and Walters 2002, Zeigler and Walters 2014), we hypothesized group size would increase over time, and that increases in group density would have positive effects on group size. Additionally, because territories in older forest stands are likely to contain relatively more large and old pines for cavity excavation and retain more helpers, we hypothesized that increases in forest stand age would have positive effects on group size.

Methods

Study species

The red cockaded woodpecker *Dryobates borealis* (RCW) is an endangered resident cooperative breeder endemic to the southern pine *Pinus* spp. forests of the United States (USFWS 2003). Habitat loss, particularly loss of longleaf

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pine *P. palustris* forests and live old pines required for nesting and roosting, was the primary historic cause of the species' decline (Jackson 1971, Conner and Rudolph 1989, 1991, Conner et al. 2001). RCWs live in social groups consisting of a breeding pair and up to four helpers, plus the current year's fledglings (Ligon 1970). Almost all females disperse following fledging, while nearly all male fledglings stay as helpers on their natal territory (Walters 1990, Walters et al. 1992). RCWs typically disperse short distances from their natal territory (~4.5 km), but occasionally will disperse much longer distances (~90 km; Conner et al. 1997). Larger groups typically have greater reproductive success and improved breeder survival due to the presence of helpers (Lennartz et al. 1987, Khan and Walters 2002). Groups also have greater reproductive success in forest with low to moderate pine density and large and old pines (e.g. >35.6 cm dbh and >60 years old) for foraging and cavity excavation (James et al. 1997, 2001, Walters et al. 2002a). Foraging RCWs almost exclusively forage on living pines, and tend to select the largest and oldest available pines (Zwicker and Walters 1999), likely due to greater arthropod prey availability relative to smaller and younger pines (Hanula et al. 2000). Cavity trees have been identified as the critical limiting resource for RCWs (Copeyon et al. 1991), in part because natural cavities can take several years to excavate (Conner and Rudolph 1995). Accordingly, short-term recovery strategies have emphasized installation of artificial cavities as a means to rapidly stabilize and increase RCW populations declining due to lack of cavity trees (Copeyon et al. 1991, Walters 1991).

Study site

The SRS, an 80 267-ha National Environmental Research Park owned and operated by the US Dept of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA. The site is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Kilgo and Blake 2005). Prior to acquisition by the Dept of Energy in 1951, the majority of the SRS was maintained in agricultural fields or recently was harvested for timber (White 2005). The US Dept of Agriculture Forest Service has managed the natural resources of the SRS since 1952 and reforested >90% of the site (White 2005). Approximately 53 014 ha of SRS has been reforested with artificially regenerated stands of loblolly *P. taeda*, longleaf and slash *P. elliottii* pines with an additional 2832 ha with pine-hardwood mixtures (Imm and McLeod 2005). The remaining 27 000 ha of forested area on the site includes bottomland hardwoods, forested wetlands/riparian areas and mixed-hardwood stands (Imm and McLeod 2005). Mixed pine-hardwood stands on SRS typically are a mixture of longleaf pine, loblolly pine and *Quercus* spp. Midstory trees typically are small *Quercus* spp., but may include mixtures of sand hickory *Carya pallida*, sweetgum *Liquidambar styraciflua* and sassafras *Sassafras albidum*. The groundcover typically is a highly variable mosaic of herbaceous plants, vines and woody stems.

In conjunction with the Dept of Energy, the Forest Service began management and research on the RCW in 1984 with the objective to restore a viable population on SRS. Under intensive management since 1985, the RCW population had grown from three active clusters with five birds (Johnston 2005) to 91 active clusters with more than 250 birds in 2017 (T. Mims unpubl.). The SRS RCW population is designated as a secondary core population in the South Atlantic Coastal Plain recovery unit and must support >250 potential breeding groups (i.e. a male and female occupying the same cluster of cavity trees) at the time of and after delisting (i.e. removal from the federal list of endangered and threatened wildlife and plants; USFWS 2003). As part of ongoing monitoring, Forest Service personnel have conducted RCW group observations and nest checks during each nesting season since 1985 to determine clutch size, nestling production, fledgling production, group size and group composition (i.e. identity and age of group members) for each cluster. All RCWs on the SRS are uniquely color-banded by Forest Service personnel. Additional information about field protocols for RCW group observation and nest checks is presented in Supplementary material Appendix 1 of the species' recovery plan (USFWS 2003).

RCW management on SRS has included prescribed fire and other mechanical and herbicide treatments to control hardwood midstory in foraging and nesting areas, installation of artificial cavities to supplement existing clusters and to foster establishment of new groups in unoccupied habitat, RCW translocations and ongoing protection of existing cavity trees (Allen et al. 1993, Haig et al. 1993, Franzreb 1997, Edwards and Costa 2004). Forest Service personnel have consistently implemented all RCW management efforts on an annual basis, as required by the RCW recovery plan (USFWS 2003). Prescribed burning occurs year-round on SRS with most areas on a return interval between three and five years. Historically, prescribed burning occurred from December to March, and by 1990s it was extended into the growing season, from mid-May through end of July. Additionally, by the 1990s, prescribed burning and other midstory control efforts were expanded to include potential RCW habitat within 4.8 km of existing clusters (Franzreb and Lloyd 2000). Between 1985 and 1996, 182 ha per year of RCW nesting and foraging habitat on SRS received some type of hardwood midstory treatment (Franzreb and Lloyd 2000). During the same period on SRS, Forest Service personnel installed 305 artificial cavities and translocated a total of 54 RCWs (21 from other populations, 33 from within the existing SRS population; Franzreb 1997).

Data acquisition and preparation

RCW demographic and cluster data

We obtained RCW group productivity data, the spatial coordinates for RCW cavity tree clusters, cluster status (active or not), and overall breeding success (number of RCW groups that produced ≥1 fledgling) between 1985 and 2017 from historic SRS monitoring data. We obtained ages of forest stands that contained an RCW cluster from the continuous inventory of stand conditions database (U.S. Forest Service unpubl.). RCW productivity metrics included annual observations of group size and fledgling production for each RCW group. Group observations were not conducted in 2008 or 2009, so we did not include these years in analyses.

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We characterized local group density for each RCW cluster that was active in each year using two metrics: 1) the number of active neighboring clusters within 800 m of a focal group during the previous year (i.e. a lagged effect of neighboring group density); and 2) the total number of RCWs in neighboring groups within 800 m of a focal group during the current year (i.e. a current effect of group density). We chose an 800-m circular buffer when calculating each group density metric as this distance is likely to include the majority of a focal group's foraging sites (Rosenberg and McKelvey 1999) and first nearest neighboring group with which a focal RCW group will interact (Engstrom and Mikusinski 1998). We used a focal group's fledgling production from the previous year to represent effects of helper retention on group sizes (Kokko and Ekman 2002). We characterized territory quality using the average age of forest stands within 800 m of a group's cavity tree cluster. We extracted and compiled all spatial data using the Neighborhood and Extraction toolsets in the Spatial Analyst toolbox in ArcGIS (ESRI 2017).

Data analysis

Modeling trends

We modeled trends in fledgling production and group size between 1985 and 2017 using general additive mixed models (GAMMs). Additive models quantify the effect of a variable using flexible smooth functions without imposing specific parametric assumptions (e.g. linearity assumed in multiple linear regression; Hastie and Tibshirani 1990). The shape of smooths and their relationship with fledgling production and group size is therefore determined by the data rather than being restricted a priori to a specific form. The degree of smoothing applied to variables is reflected by the degrees of freedom, which can be loosely interpreted as the number of parameters used to fit the smooth function (Fewster et al. 2000). As the degrees of freedom are increased, the smooth gains flexibility and can accommodate increasingly nonlinear trends and fluctuations. The degrees of freedom for a given smooth can be specified to reflect hypothesized relationships, including linear trends, gradual and smooth trends, or nonlinear trends with abrupt fluctuations (Fewster et al. 2000). Alternatively, cross-validation can be used to automatically estimate the optimal degrees of freedom (Zuur et al. 2009). When fixing the degrees of freedom, Fewster et al. (2000) recommended setting the degrees of freedom to roughly 0.3 times the length of the time series, or based on specific objectives. We set the degrees of freedom to 16 for smoothed effects of year in both GAMMs because our objective was to capture short-term (e.g. four years) fluctuations within the nonlinear trends in group size and fledgling production. We used cross-validation to estimate the degrees of freedom for all other smooth terms included in subsequent GAMMs.

We fit two separate GAMMs to model trends in RCW fledgling production and group sizes. In both GAMMs, we included smoothed functions for interactions among year, the number of active neighboring clusters within 800 m during the previous year, the sum of RCW group sizes within 800 m during the current year, and the average age of forest stands within 800 m of a group's cavity tree cluster. In the fledgling production trend GAMM, we also fit a smoothed interaction between average age of forest stands within 800 m and group size during the current year to account for positive effects of group size on reproductive success. In the group size trend GAMM, we also fit a smoothed interaction between average age of forest stands within 800 m and a focal group's fledgling production in the previous year to account for fledgling retention because RCWs are philopatric. To examine potential moderating effects of forest stand age in both GAMMs, we predicted effects for the number of active neighboring clusters within 800 m during the previous year and the sum of RCW group sizes within 800 m during the current year across stand ages of 40, 60, 80 and 100 years. We used stand age classes of 40, 60, 80 and 100 years within 800 m to estimate predicted effects based on age classes defined in the RCW recovery plan and previous research (USFWS 2003). Additionally, we predicted effects for a focal group's fledgling production in the previous year and a focal group's size in the current year on average group size and fledgling production, respectively, across stand ages of 40, 60, 80 and 100 years. Finally, for both GAMMs, we used post hoc contrasts to compare predicted effects for the number of active neighboring clusters within 800 m during the previous year and the sum of RCW group sizes within 800 m during the current year across average stand ages of 40, 60, 80 and 100 years. We included cluster ID as a random effect in both GAMMs to account for varying sample sizes and repeated measures for each cluster. We tested each model's residuals for spatial autocorrelation using Moran's I statistic calculated at 22 distance bands ranging between 500 and 20 000 m (Dormann et al. 2007). We did not detect significant temporal autocorrelation in residuals from either GAMM (rho values of −0.01 and 0.01, in the fledgling production and group size models, respectively), likely due to inclusion of year and lagged effects of specific covariates (Knape 2016). Therefore, we did not fit trend models with an autoregressive correlation structure. We conducted all analyses in the R statistical environment using the contributed packages 'mgcv' (Wood 2018) to fit GAMM models, 'emmeans' (Lenth 2019) to conduct post hoc contrasts, and 'pgirmess' (Giraudoux et al. 2018) for testing model residuals for spatial autocorrelation.

Results

Total active RCW clusters, clusters with successfully breeding RCW groups, and overall group productivity metrics steadily increased from 1985 to 2017 on SRS (Fig. 1). Annual fledgling production averaged 1.7 (SD = 1.2) and ranged from 0 to 5 fledglings per potential breeding group. Fledgling production trends exhibited oscillations over 2–3 year periods from 1985 to 1994, but longer-term evaluation suggests stabilization over time rather than a decrease; oscillations also dampened over time (Fig. 2). Annual size of potential breeding groups (i.e. the breeding pair plus any helpers) averaged 2.5 (SD = 0.9) and ranged from two to seven individuals per group. Group size exhibited abrupt fluctuations over 2–3 year periods from 1985 to 1994, but longer term evaluation suggests a general increase in average group size from 1985 to 1994, followed by declines from 1995 to 2007, and a period of steady increase after 2010 (Fig. 2).

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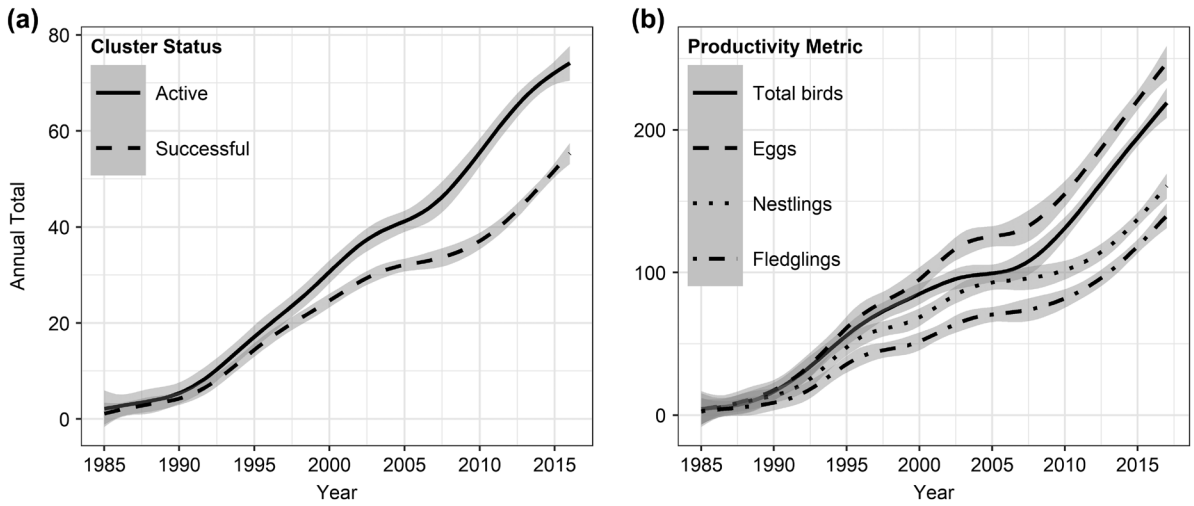


Figure 1. Smooths (black lines) and 95% confidence bands (gray bands) for annual population-level trends in red-cockaded woodpecker (a) cluster status and (b) productivity on the Savannah River Site, SC, between 1985 and 2017.

Overall, average fledgling production and group size were affected more by increases in neighboring group density and neighboring group sizes than by the average age of forest stands within 800 m of a group's cavity tree cluster (Fig. 3, 4, Supplementary material Appendix 1 Table A1, A2). For both fledgling production and group size models, Moran's I estimates were <0.01 with p-values >0.10 across all distance bands, indicating no significant spatial autocorrelation in model residuals at any distance tested (Supplementary material Appendix 1 Fig. A1). Fledgling production

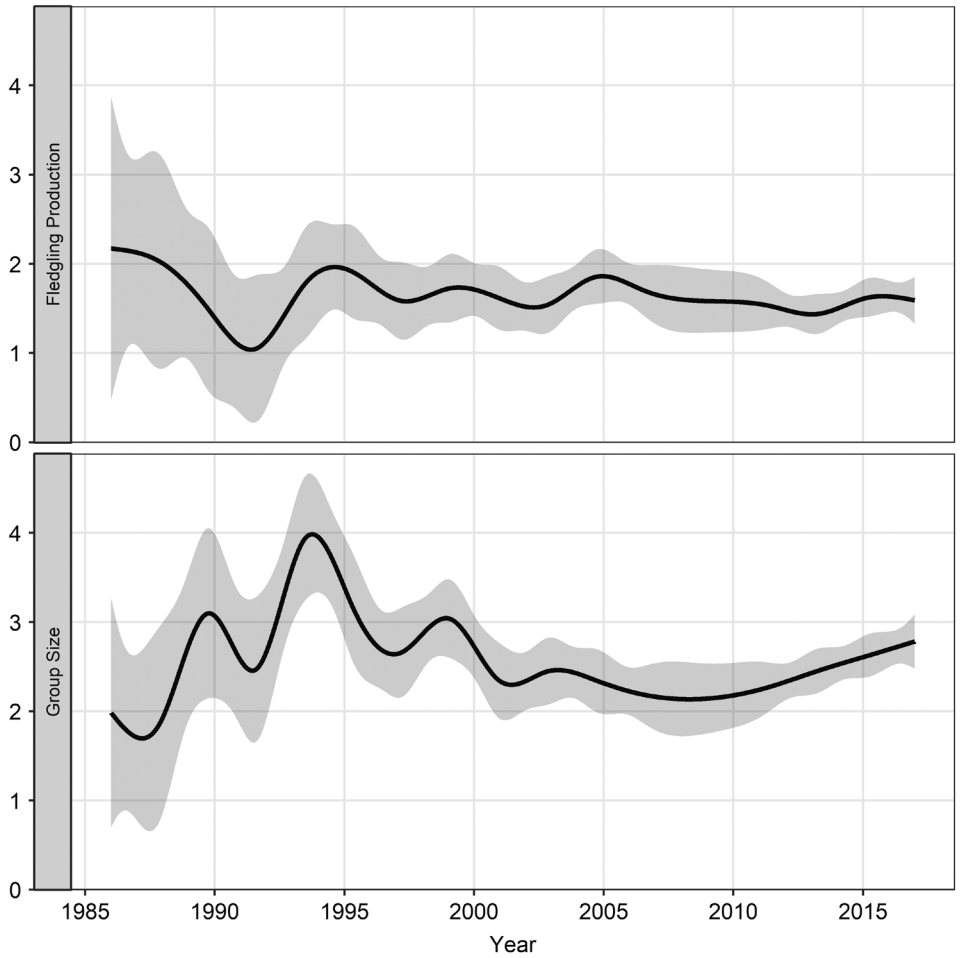


Figure 2. Average fledgling production and group size of red-cockaded woodpeckers on the Savannah River Site, SC, between 1985 and 2017.

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increased with the number of active clusters <800 m during the previous year and the size of a focal group in the current year, but declined with increases in the sum of neighboring group sizes <800 m in the current year (Fig. 3b). Fledgling production increased with group size when average stand ages within 800 m of a group's cavity tree cluster were 60, 80 and 100 years, but fledgling production decreased slightly for groups of four when the average stand age was 40 years (Fig. 3b). Post hoc contrasts indicated no significant differences in effects of active clusters in the previous year or the sum of neighboring group sizes in the current year on average fledgling production (Table 1).

Focal group size increased with the number of active clusters <800 m during the previous year, the sum of neighboring group sizes <800 m in the current year, and fledglings produced in the current year (Fig. 4b). The positive effects of active clusters, sum of neighboring group sizes, and fledgling production on the size of a focal group were consistent across average stand ages of 40, 60, 80 and 100 years (Fig. 4b). Post hoc contrasts indicated no significant differences in the effect of active clusters in the previous year or the sum of neighboring group sizes in the current year on average group size across average stand ages of 40, 60, 80 and 100 years (Table 2).

Discussion

Our results indicate RCW fledgling production and group size trends over the long-term depend more on local group density and group sizes, respectively, than the age of forest stands containing a group's cavity tree clusters. Increases in local group density facilitate demographic connectivity that leads to larger group sizes, but also to heightened competition and reduced fledgling production that is not mitigated by increases in average stand age over the time. Considering the relatively wide confidence intervals for effects of stand age classes on fledgling production and group size, it is possible that effects of stand age could be weaker or stronger than predicted. Nonetheless, the relatively small differences in fledgling production and group size trends across stand ages over the long-term likely reflect that, as a social species with limited dispersal, RCWs may exhibit stronger and more consistent responses to neighboring group density and interactions with neighboring groups than to increases in forest age over the long-term (Walters et al. 1999, Zeigler and Walters 2014, Garabedian et al. 2018b). If average stand age moderated effects of either group density or neighboring group size on a focal group's fledgling production or size, then we would have observed clear differences in fledgling production and focal group sizes between young and old stands (40 and 100-year-old stands, respectively, in our case). Consistent with our hypothesis, increases in RCW group density over time likely leads to a more competitive social environment that equally impacts all RCW groups (Ferrer and Donazar 1996, Both 1998, Newton 1998), and this may be the primary factor regulating fledgling production in young and old stands alike. Thus, with ongoing habitat management (e.g. prescribed burning and maintenance

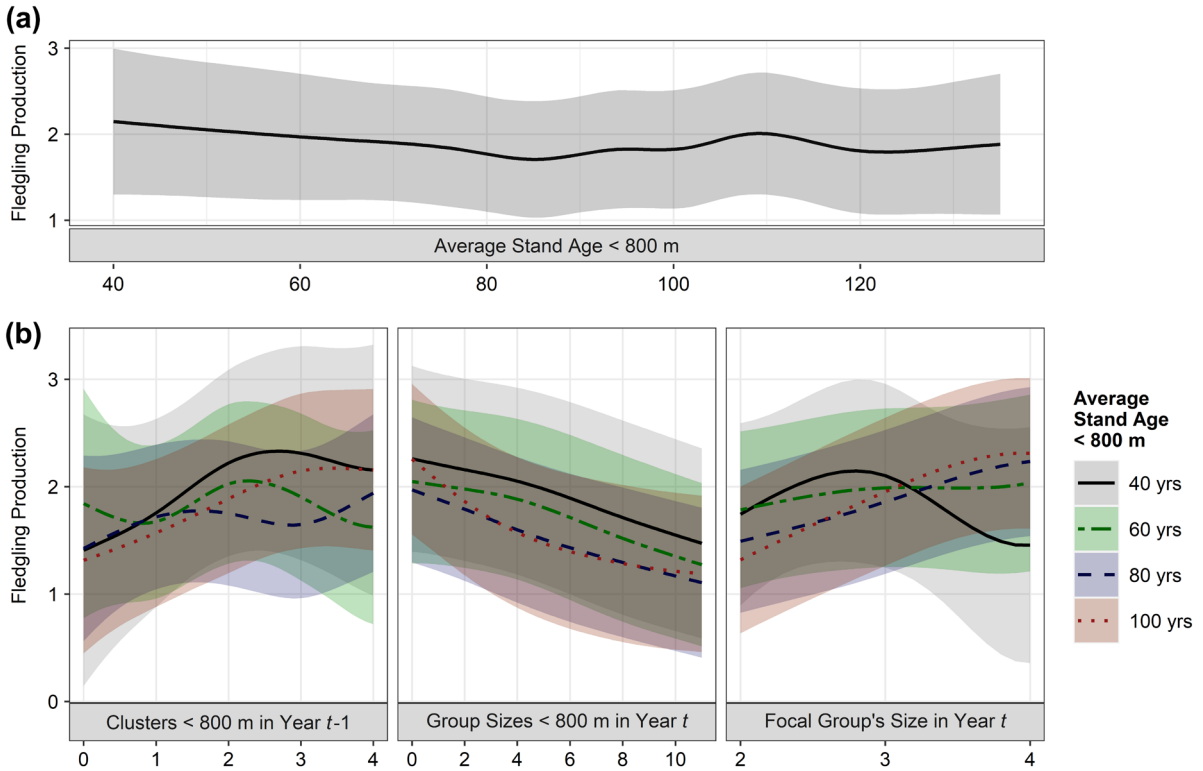


Figure 3. Smooths (line types) and 95% confidence bands (shaded bands) for (a) effects of the average age of forest stands within 800 m of a group's territory on red-cockaded woodpecker fledgling production and (b) changes in fledgling production in response to active clusters within 800 m during the previous year (left panel), sum of all neighboring group sizes within 800 m in the current year (center panel), size of the focal group in the current year (right panel) across forest stands with average ages of 40, 60, 80 and 100 years old within 800 m of a group's territory on the Savannah River Site, SC.

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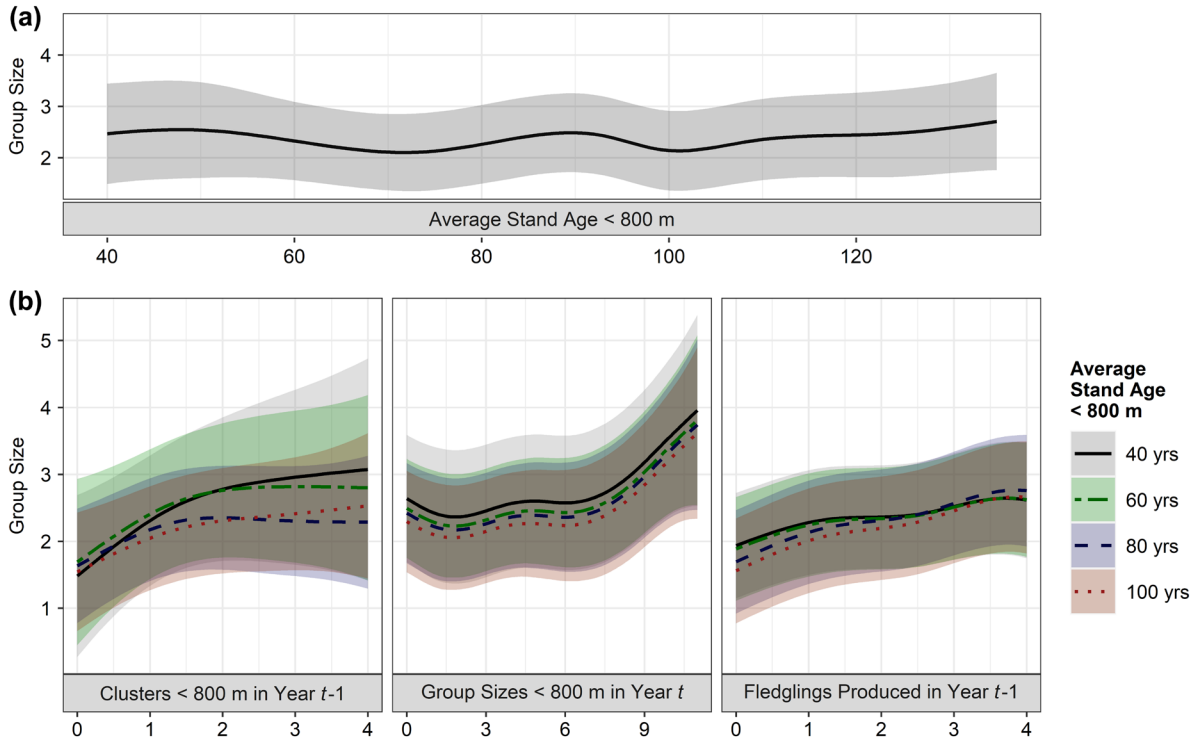


Figure 4. Smooths (line types) and 95% confidence bands (shaded bands) for (a) effects of the average age of forest stands within 800 m of a group's territory on red-cockaded woodpecker group size and (b) changes in group sizes in response to active clusters within 800 m during the previous year (left panel), sum of all neighboring group sizes within 800 m in the current year (center panel), and a focal group's fledgling production during the previous year (right panel) across forest stands with average ages of 40, 60, 80 and 100 years old within 800 m of a group's territory on the Savannah River Site, SC.

of large and old pines; USFWS 2003), long-term RCW population trends will be driven primarily by changes in local group density conditions and group sizes rather than increases in forest stand age.

Contrary to our hypothesis, the oscillatory pattern in fledgling production related to density-dependent competition, and was not moderated by forest age. We hypothesized that increases in forest age would mitigate effects of group density and heightened competition on fledgling production, so we expected increased fledgling production with increasing forest age. Such a trend was not evident, although confidence intervals suggest fledgling production may have stabilized after 2005. This highlights the importance of understanding long-term effects of density in recovery of group-living social species. Habitat management directed at maintaining large pines and minimal hardwood midstory encroachment may be more likely than increases in forest age to mitigate effects of competition on fledgling production. Over the short-term (e.g. periods of 2–5 years), habitat structure has been linked to reproductive success (James et al. 1997, 2001, Walters et al. 2002a). However, our results support previous studies that have shown a focal group's size to be even more important to fledgling production than habitat structure in the SRS RCW population (Garabedian et al. 2017,

Table 1. Post hoc contrasts and Tukey groupings for effects (±SE) of the sum of group sizes <800 m in the current year, the sum of active clusters <800 m in the previous year, and a focal group's size in the current year on fledgling production of a focal red-cockaded woodpecker group across average stand ages of 40, 60, 80 and 100 years within 800 m of a focal group's cavity tree cluster on Savannah River Site, SC, between 1985 and 2017.

Variable	Average stand age	β	Tukey[a]
Group sizes <800 m in year *t*	40	−0.148 ± 0.06	A
Group sizes <800 m in year *t*	60	−0.137 ± 0.064	A
Group sizes <800 m in year *t*	80	−0.197 ± 0.038	A
Group sizes <800 m in year *t*	100	−0.166 ± 0.046	A
Active clusters <800 m in year *t* − 1	40	0.141 ± 0.190	A
Active clusters <800 m in year *t* − 1	60	0.137 ± 0.113	A
Active clusters <800 m in year *t* − 1	80	0.172 ± 0.123	A
Active clusters <800 m in year *t* − 1	100	0.131 ± 0.142	A
Focal group's size in year *t*	40	0.335 ± 0.101	A
Focal group's size in year *t*	60	0.313 ± 0.130	A
Focal group's size in year *t*	80	0.402 ± 0.175	A
Focal group's size in year *t*	100	0.348 ± 0.167	A

[a] Tukey groupings apply across levels of average stand age within each variable.

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Table 2. Post hoc contrasts and Tukey groupings for effects (±SE) of the sum of group sizes <800 m in the current year, the sum of active clusters <800 m in the previous year, and fledglings produced by a focal group in the previous year on the size of a focal red-cockaded woodpecker group across average stand ages of 40, 60, 80 and 100 years within 800 m of a focal group's cavity tree cluster on Savannah River Site, SC, between 1985 and 2017.

Variable	Average stand age	β	Tukey[a]
Group sizes <800 m in year t	40	0.278 ± 0.180	A
Group sizes <800 m in year t	60	0.269 ± 0.149	A
Group sizes <800 m in year t	80	0.264 ± 0.121	A
Group sizes <800 m in year t	100	0.232 ± 0.130	A
Active clusters <800 m in year $t-1$	40	0.180 ± 0.093	A
Active clusters <800 m in year $t-1$	60	0.173 ± 0.081	A
Active clusters <800 m in year $t-1$	80	0.167 ± 0.075	A
Active clusters <800 m in year $t-1$	100	0.160 ± 0.075	A
Fledglings produced in year $t-1$	40	0.133 ± 0.180	A
Fledglings produced in year $t-1$	60	0.053 ± 0.114	A
Fledglings produced in year $t-1$	80	0.136 ± 0.107	A
Fledglings produced in year $t-1$	100	0.145 ± 0.107	A

[a] Tukey groupings apply across levels of average stand age within each variable.

2019). Our results show that over the long-term, declines in fledgling production are primarily linked to increases in neighboring group sizes, reflecting increased competition and crowding effects that are not moderated by increases in forest age. The relatively greater importance of group density and group size to fledgling production compared to average forest age may also explain why the SRS RCW population has been healthy and growing even when previous studies have shown <30% of RCW habitat satisfies current USFWS foraging habitat guidelines (Garabedian et al. 2014b).

For RCWs, increased demographic connectivity facilitated by increases in group density can both mitigate and exacerbate effects of competition on long-term fledgling trends. Heightened competition among neighboring groups can be costly to fledgling production due to greater investment in territorial defense (Garabedian et al. 2018a). Contrary to our hypothesis, the negative relationships between fledgling production and sum of neighboring group sizes within 800 m in the current year across stand ages shows that, with ongoing habitat management to maintain ideal forest structure (i.e. open canopies with some large pines and minimal hardwood midstory encroachment), increases in average stand age will not be likely to offset effects of competition on fledgling production over the long-term. The benefits to group sizes from increased demographic connectivity under high group density conditions may outweigh costs to fledgling production from competition. For instance, the positive relationship between neighboring group density and group size may improve breeder survival at high density by indirectly increasing group sizes (Khan and Walters 2002). The positive lagged effect of neighboring group density on fledgling production we documented likely reflects an indirect benefit of breeder replacement and dispersal success that maintains larger groups. Carrie et al. (1999) observed a beneficial social interaction when releasing individuals in close proximity to resident birds. However, our results indicate these indirect benefits are unlikely to entirely offset effects of competition on fledgling production.

A minimum number of neighboring groups needed to maintain population viability may apply generally to the persistence of small populations of cooperative breeding species, even when increases in density reduce productivity over the long-term. Even relatively small increases in local group density are likely to promote demographic connectivity that benefits group sizes (Walters et al. 1999). Based on results from our study, RCW group sizes and persistence are likely to be maximized when there are at least two active clusters and six individuals within the local neighborhood. Consistent with our hypothesis, this demographic connectivity should improve the likelihood that juveniles produced by neighboring groups will disperse to become helpers in groups that did not produce any fledglings. Thus, with at least two active groups or six individual RCWs within the local neighborhood, retention of fledglings as helpers becomes less important to a focal groups' size because improved demographic connectivity will promote larger group sizes. Clumping of territories is critical to persistence of RCW populations, as it facilitates dispersal of non-breeders into breeding vacancies and recruitment clusters (Letcher et al. 1998, Walters et al. 2002b). If the minimum number of neighboring groups and individuals is not reached, the primary means of increasing RCW group size without reliance on group augmentation (e.g. through translocation) will be fledgling retention.

Our results indicate that once stand ages reach 40 years, with ongoing habitat management, provision of dense aggregates of recruitment clusters can be an effective strategy for establishing and maintaining large group sizes over the long-term. In some species, experimentally increasing density of nest boxes creates an ecological trap if food is limited (Mänd et al. 2009), potentially due to differences in microclimatic conditions between young and old stands (Chen et al. 1993), but this is unlikely for RCWs because arthropod prey availability is similar in relatively young and old forests (Hanula and Engstrom 2000). Further, dense aggregations of recruitment clusters where baseline habitat conditions are satisfied reduce the need to disperse through fragmented habitat, which is costly for RCWs and other cooperative breeders (Walters et al. 1999, Kesler and Walters 2012). As an example, reintroduced brown treecreepers *Climacteris picumnus* were more vulnerable to predation during longer flights to reach restored areas (Bennett et al. 2013). Although RCWs are known to disperse through heterogeneous matrix conditions, it is likely to be more costly if they must also do

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so without gaining information about their neighbors. However, improved spatial guidance for strategic placement of recruitment clusters is needed to ensure the benefits to group sizes from increased demographic connectivity we identified are achieved on the landscape without increasing the rate of captured clusters (i.e. two cavity tree clusters occupied by individuals of the same social group; USFWS 2003).

Group living is characteristic of social species, but living in groups at high density has both advantages and disadvantages for group size and productivity trends over the long-term. Our results indicate group size and fledgling production trends in the SRS RCW population are driven primarily by group density and the associated improvement in demographic connectivity that benefits group sizes rather than by increases in forest age over the long-term. Thus, RCW may be less effective as an umbrella species for old, open and fire maintained forest stands than previously thought (McKellar et al. 2015, Johnson et al. 2017). For RCWs, social factors that can be highly advantageous for group sizes can also result in a significant reduction in fledgling production, independent of forest age. Our study indicates that even increases in forest age over the long-term do not override the effects of group density on group size and productivity trends.

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Supplementary material (available online as Appendix wlb-00574 at <www.wildlifebiology.org/appendix/wlb-00574>). Appendix 1.

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