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Group size mediates effects of intraspecific competition and forest structure on productivity in a recovering social woodpecker population

J. E. Garabedian[1], C. E. Moorman[2], M. N. Peterson[2] & J. C. Kilgo[1]

1 USDA Forest Service Southern Research Station, New Ellenton, SC, USA

2 Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Raleigh, NC, USA

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cooperative breeder; endangered species; indirect effects; population density; prescribed fire; structural equation model; woodpecker.

Correspondence
James E. Garabedian, USDA Forest Service Southern Research Station, P.O. Box 700, New Ellenton, SC, USA.
Email: james.garabedian@usda.gov

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Abstract

Conservation of endangered social wildlife in disturbance-prone forests is challenging because direct and indirect effects of management strategies developed at the time of species' listing when population density is low may change under high-density conditions in locally recovered populations. Here, we used piecewise structural equation modeling to evaluate direct and indirect drivers of productivity in the federally endangered cooperatively breeding red-cockaded woodpecker *Dryobates borealis* (RCW) on Savannah River Site, South Carolina, USA. We estimated direct and indirect relationships among group size, neighboring group sizes, fledgling production, density of cavity tree clusters occupied by RCWs, area satisfying threshold criteria of ≥22 stems ha^{-1} of pines ≥35.6 cm diameter at breast height (dbh), <1.4 m^2 ha^{-1} basal area (BA) of hardwoods 7.6–22.9 cm dbh, and <6% hardwood canopy cover, and area treated with prescribed fire, and tested whether group size mediated indirect effects of area satisfying threshold criteria on fledgling production. Increases in area with ≥22 stems ha^{-1} of pines ≥35.6 cm dbh and <1.4 m^2 ha^{-1} BA of hardwoods 7.6–22.9 cm dbh, and area treated with prescribed fire, but not area with <6% hardwood canopy cover, had direct positive effects on group size. Group size and area treated with prescribed fire, but not area satisfying threshold criteria, had direct positive effects on fledgling production. The direct effect of neighboring group sizes on fledgling production was negative and smaller relative to the direct positive effect of group size on fledgling production. Overall, our results indicate positive direct effects of group size on fledgling production outweighed negative direct effects of neighboring group sizes, and that group size mediated positive indirect effects of area satisfying structural threshold criteria on fledgling production. These findings indicate that ongoing forest management aimed to increase area with ≥22 pines ha^{-1} ≥35.6 cm dbh and <1.4 m^2 ha^{-1} BA of hardwoods 7.6–22.9 cm dbh will promote large group sizes, which in turn improve fledgling production and offset costs of heightened competition with neighboring groups under high-density conditions. Additionally, positive effects of area treated with prescribed fire on RCW group size and fledgling production indicate prescribed fire has unique contributions to woodpecker productivity, likely via direct effects on forest structure and potentially indirect effects on arthropod prey available to foraging RCWs. By simultaneously accounting for multiple drivers of productivity in social wildlife, our study contributes to the understanding of how increases in social wildlife population sizes can alter previously documented habitat-fitness relationships.

Introduction

Disentangling direct and indirect drivers of productivity for wildlife is important for the recovery of endangered species (Wootton, 1994; Darst *et al*., 2013). Studies explicitly distinguishing drivers as direct or indirect provide information critical to understanding whether changes in habitat conditions directly affect species' productivity, or if effects of habitat conditions are indirect and mediated by other factors (Grace, 2008). For instance, frequent prescribed fire may alter wildlife productivity directly through effects on vegetation structure and composition (Engstrom, 2010), or indirectly through mediating effects on arthropod prey (Kim & Holt, 2012). Despite relationships between habitat conditions and wildlife productivity typically involving causal chains and networks, conventional analytical approaches assume predictors have direct effects (Graham, 2003), thus presenting a challenge in anticipating how changes in habitat conditions and disturbance processes may impact the recovery of endangered species.

Determining whether habitat conditions or population density directly or indirectly influence habitat-fitness relationships for social species has been a challenge, in part because changes in behaviors and group dynamics at high population density may decouple habitat-fitness relationships observed at low population density or reflect habitat-fitness relationships that underestimate the importance of social behaviors (Greene & Stamps, 2001). Ongoing habitat management aimed at restoring and maintaining desired conditions often leads to increases in population density (Porzig *et al*., 2014), which may result in heightened competition in group-territorial species, confounding habitat-fitness relationships observed at lower densities (Brown, 1969). Additionally, because population density and habitat quality often correlate positively with group size (van Balen, 1973; Luck, 2002), the effects of habitat quality on productivity in social species may be confounded by group size effects as well as population density. For instance, social interactions can be beneficial regardless of habitat quality (Scott & Lee, 2012) by improving dispersal success (Barve *et al*., 2020) and promoting larger group sizes (Krause & Ruxton, 2002). However, increases in competition that covary with population density may offset the benefits of habitat quality and larger group sizes to reproductive success (Brouwer *et al*., 2009).

In this study, we used structural equation modeling (SEM; Shipley, 2000) to partition direct and indirect relationships among group size, population density, habitat quality, prescribed fire, and group productivity in the federally endangered red-cockaded woodpecker *Dryobates borealis* (RCW) on Savannah River Site (SRS), South Carolina, USA. The RCW is a group-territorial and cooperatively breeding species endemic to the fire-maintained pine *Pinus* spp. forests of the southeastern United States (U.S. Fish and Wildlife Service, 2003). RCWs live in social groups consisting of a breeding pair and up to five helper individuals (non-breeding RCWs that assist with rearing young, cavity tree maintenance, and territorial defense; U.S. Fish and Wildlife Service, 2003). RCW population dynamics are largely driven by the distribution of cavity tree clusters (i.e. an aggregate of cavity trees; hereafter, cluster) occupied by RCW groups, rather than the number of individuals, because a large pool of helper individuals is available to replace breeders that die (Walters, Doerr & Carter, 1988). Accordingly, population sizes required for RCW recovery are based on the number of clusters occupied by RCW groups (U.S. Fish and Wildlife Service, 2003).

The SEM analytical framework is ideal for modeling RCW reproductive success because productivity is simultaneously influenced by the density and distribution of clusters and the size of RCW groups occupying clusters (Conner *et al*., 1999, 2004; Garabedian *et al*., 2019*a*), forest structure (Walters *et al*., 2002), and the extent and frequency of prescribed fire (James, Hess & Kufrin, 1997). Group sizes are positively influenced by fledgling retention (i.e. philopatry; Walters *et al*., 1988), and larger groups typically have greater fledgling production because of the presence of helpers (Lennartz, Hooper & Harlow, 1987; Conner *et al*., 2004). Group sizes, cluster density, and fledgling production also tend to increase with the area of forest characterized by low to moderate density (stems ha^{-1}) of large and old pines [e.g. ≥35.6 cm diameter at breast height (dbh) that are >60 years old] and minimal hardwood midstory encroachment (James *et al*., 1997, 2001; Walters *et al*., 2002). Furthermore, studies indicate increases in RCW group size (Khan & Walters, 2002) and neighboring cluster density and neighboring group sizes (i.e. the number of clusters and the number of RCWs occupying clusters within 800 m of a given RCW group, respectively) have direct positive and negative effects, respectively, on fledgling production (Garabedian *et al*., 2018, 2019*a*). However, little research has explored whether group size mediates effects of forest structure and neighboring group sizes on fledgling production (i.e. whether forest structure and neighboring group sizes directly affect the RCW group size, which in turn influences fledgling production), and, if so, whether effects mediated by group size are positive or mixed and offsetting. For instance, group size may simultaneously mediate offsetting positive and negative effects of neighboring group sizes on fledgling production whereby neighboring group sizes can increase the size of a given RCW group (mediated effect on fledgling production is positive) but also increase competition (mediated effect on fledgling production is negative).

As RCW populations expand into new areas with ongoing recovery efforts, more reliable information is needed on the relationships among group size, neighboring cluster density and neighboring group sizes, forest structure, and prescribed fire, and whether group size mediates effects of forest structure and neighboring group sizes on fledgling production. Although previous studies of RCW habitat-fitness relationships have elucidated forest structural characteristics that guide range-wide management of foraging and nesting sites (U.S. Fish and Wildlife Service, 2003), it is becoming apparent that forest structure alone does not consistently improve group productivity (Spadgenske *et al*., 2005; McKellar *et al*., 2014; Garabedian *et al*., 2017, 2019*c*). The lack of consistent relationships between forest structure and RCW productivity may be due to mediating effects of group size (Garabedian *et al*., 2017, 2019*a*,*c*). In other cooperative breeders, group size effects outweigh effects of territory quality on fledgling production (Doerr & Doerr, 2007), suggesting positive effects of forest structure on RCW fledgling production may be indirect and mediated by group size. Additionally, increases in neighboring cluster density in response to ongoing forest management and provision of artificial cavities (Allen, 1991) may have positive effects on group sizes (Garabedian *et al*., 2019*a*), but may simultaneously reduce productivity through heightened intraspecific competition (Garabedian *et al*., 2018). Understanding the effects of neighboring cluster density may be especially important for reintroduction efforts where RCWs are introduced into small and isolated forests that provide few, if any, dispersal opportunities. If RCWs are unable to find suitable dispersal destinations, the benefits dispersing helper individuals confer on population persistence (i.e. replacement of vacant breeding positions by dispersing helper individuals; Walters *et al*., 1988) and reproductive success could be minimized, thus hindering species' recovery.

Materials and methods

Study site

The SRS, an 80 267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina. The site is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Kilgo & Blake, 2005). Prior to acquisition by the Department of Energy in 1951, the majority of the SRS was maintained in agricultural fields or recently was harvested for timber. The U.S. Department 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 *P. palustris*, and slash *P. elliottii* pines with an additional 2832 ha with pine-hardwood mixtures (Imm & 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. The remaining 27 000 ha of forested area on the site includes bottomland hardwoods, forested wetlands/riparian areas, and mixed-hardwood stands (Imm & McLeod, 2005).

In conjunction with the Department of Energy, the Forest Service began intensive management and research on the RCW in 1984 with the objective to restore a viable population on SRS. 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, with or without helpers) at the time of and after delisting (i.e. removal from the federal list of endangered and threatened wildlife and plants; U.S. Fish and Wildlife Service, 2003). Under intensive management since 1985, the SRS RCW population has grown from 3 clusters occupied by 5 individual RCWs (Johnston, 2005) to 140 clusters occupied by over 500 birds in 2020 (R. Geroso, pers. comm.). As part of ongoing monitoring, Forest Service personnel have conducted RCW group observations and nest checks during each nesting season since 1985 to monitor clutch size, nestling production, fledgling production, group size, and group composition for each cluster.

The SRS RCW population has expanded dramatically while group-level productivity has fluctuated over several decades of intensive management (Fig. 1; Franzreb, 1997). RCW management on SRS has included prescribed fire and other mechanical and herbicide treatments to reduce hardwood

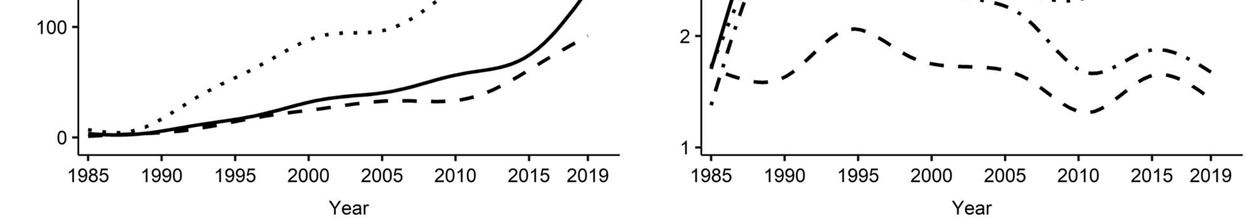

Figure 1 Trends in annual size (a) and productivity (b) metrics for the red-cockaded woodpecker (RCW) population on Savannah River Site, South Carolina, USA, between 1985 and 2020. Annual size metrics include total active clusters (i.e. aggregates of cavity trees occupied by one or more RCWs), total successful clusters (active clusters that produced ≥1 fledgling), and total individual RCWs observed during each breeding season (No. birds). Productivity metrics include annual means of clutch size, nestlings, fledglings, and number of RCWs (Group size) per woodpecker group. Plotted lines reflect locally estimated smoothed trends in annual RCW population size and productivity metrics obtained from Savannah River Site RCW annual monitoring data (U.S. Forest Service, unpubl. data).

midstory in foraging and nesting sites, installation of artificial cavities to supplement existing clusters and to foster establishment of new RCW groups in unoccupied areas, translocations (i.e. capture and transport of RCWs between populations, typically to augment small and isolated populations), and ongoing protection of cavity trees (Allen, Franzreb & Escano, 1993; Haig, Belthoff & Allen, 1993; Franzreb, 1997; Edwards & Costa, 2004). Prescribed fire is applied year-round on SRS with most areas on a return interval between 3 and 5 years. Historically, prescribed fire was applied from December to March, and by the 1990s it was extended into the growing season, from May to July. Additionally, by the 1990s, prescribed fire and other hardwood midstory reduction efforts were expanded to include areas within 4.8 km of existing RCW clusters. Between 1985 and 1996, 182 ha per year of RCW foraging and nesting sites on SRS received prescribed fire or other types of hardwood midstory treatments (Franzreb & Lloyd, 2000). During the same period on SRS, Forest Service personnel installed 305 artificial cavities and translocated 54 RCWs (21 from other populations, 33 from within the existing SRS population; Franzreb, 1997).

Piecewise SEM

Piecewise SEM is a multivariate analytical framework that facilitates simultaneous evaluation of multiple *a priori* hypotheses, each represented by individual models (i.e. component models), in a single modeling process (Lefcheck, 2016). A significant advantage of piecewise SEM is the ability to test direct and indirect effects (Hoyle, 2012). Direct effects are simply the path coefficients for a given predictor and response variable. Indirect effects reflect the magnitude of the effect of the first variable on the last variable along a compound path, accounting for effects of the intermediate variable(s) along the path (i.e. mediating variables), and are calculated as the product of coefficients along compound paths. We used piecewise SEM to test all direct and indirect relationships associated with hypotheses in this study.

Conceptual path model hypotheses

Based on our *a priori* hypotheses described in the sections below, we developed a single conceptual model to test against group-level empirical data, distinguishing our confirmatory approach from more exploratory applications of SEM (Grace & Pugesek, 1998). Following Grace *et al*. (2012), we developed a conceptual path model reflecting *a priori* hypotheses about relationships among RCW group size, neighboring group sizes, neighboring cluster density, forest structure, area receiving prescribed fire, and fledgling production based on research compiled in the RCW recovery plan (U.S. Fish and Wildlife Service, 2003) and additional RCW research published after the species' recovery plan (Table 1; Fig. 2; Supporting Information Table S1).

Forest structure

Given the narrow habitat requirements of RCWs and previously reported correlations between group size and area of forest characterized by low to moderate density of pines ≥35.6 cm dbh, minimal hardwood midstory encroachment, and minimal hardwood canopy cover (U.S. Fish and Wildlife Service, 2003, and references therein), we hypothesized increases in the area of forest reflecting these structural conditions (hereafter, forest structure) would have direct positive effects on group size [hypothesis (h)1]. However, based on the lack of consistent relationships between forest structure and fledgling production (Spadgenske *et al*., 2005; Garabedian *et al*., 2014, 2019*c*), we hypothesized forest structure would not be related to fledgling production (h2). Although explicit tests of no effect are uncommon in wildlife research, testing the hypothesis of no effect for h2 was important considering the confirmatory nature of the SEM and related goal of evaluating the relative importance of all factors, rather than removing factors with little support from further consideration (Grace, 2008; Dochtermann & Jenkins, 2011).

Table 1 Definitions of variables used to fit component models in a piecewise structural equation model of red-cockaded woodpecker (RCW) productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year)

Variable name[a]	Variable type	Definition
Group size	Predictor and response	Number of individuals occupying a RCW group's cluster in the current year
Fledgling production	Response	Number of fledglings produced by an RCW group in the current year
Neighboring group sizes	Predictor	Number of individual RCWs occupying clusters within 800 m of a RCW group in the current year
Neighboring cluster density$_{t-1}$	Predictor	Number of active RCW clusters within 800 m of a RCW group in the previous year
Fledglings$_{t-1}$	Predictor	Number of fledglings produced by a RCW group in the previous year
HA LP	Predictor	Number of hectares with ≥22 pines ha^{-1} that are ≥35.6 cm dbh within 800 m of a RCW group
HA HWMID	Predictor	Number of hectares with <1.4 m^2 ha^{-1} basal area of hardwoods 7.6–22.9 cm dbh within 800 m of a RCW group
HA HWCOV	Predictor	Number of hectares with <6% hardwood canopy cover within 800 m of a RCW group
HA burned	Predictor	Number of hectares treated with prescribed fire within 800 m of a RCW group

HA, hectare; LP, large pines; HWMID, hardwood midstory; HWCOV, hardwood canopy cover.
[a] $t-1$ = 1 year prior to current year; current year = 2018, 2019, and 2020.

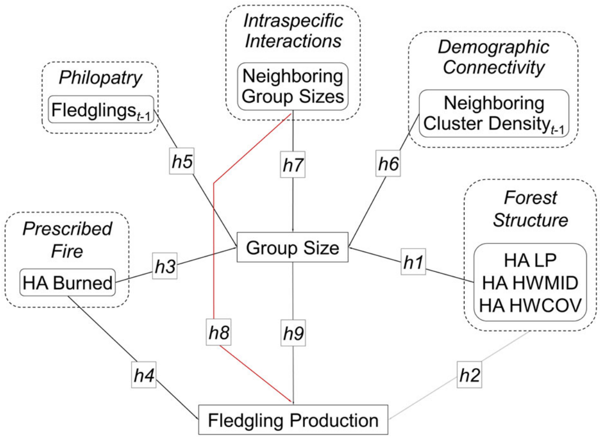

Figure 2 Conceptual path model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 ($n = 63$ during each year). Square boxes denote response variables for each component model, dashed round boxes denote predictor groups, and round boxes denote predictors. Lines with arrows (i.e. paths) point from predictors to responses, and line color reflects the hypothesized direction of effects (positive = black, negative = red; gray = negligible effects). Square boxes overlaid on individual paths denote *a priori* hypotheses for direct effects associated with each path (denoted as *h* with a numbered suffix, reflecting *a priori* hypotheses described in main text outlining conceptual path model hypotheses). Descriptions for all *a priori* hypotheses are in Supporting Information Table S1. Definitions for all variables are in Table 1.

Prescribed fire

Frequent prescribed fire is a well-established management tool used to maintain specific forest conditions for RCWs (Conner, Rudolph & Walters, 2001). Therefore, we hypothesized increases in area (number of hectares) treated with prescribed fire would have direct positive effects on group size (h3) and fledgling production (h4).

Demographic connectivity and philopatry

RCWs are a social species with limited dispersal, and increases in neighboring cluster density improve dispersal success (i.e. demographic connectivity), and by extension group sizes (Walters, Copeyon & Carter, 1992; Pasinelli & Walters, 2002). Therefore, we hypothesized increases in the number of neighboring clusters during the previous year would have direct positive effects on group size (h5). Given RCWs are philopatric (Walters *et al.*, 1988), we hypothesized fledgling production within a given RCW group during the previous year would have direct positive effects on group size (h6).

Neighboring group sizes and group size

Given larger neighboring groups are likely to produce more fledglings, and juvenile RCWs are more likely to disperse to neighboring clusters when group size on their natal territory is large (Hooper & Lennartz, 1983; Engstrom & Mikusinski, 1998; Herbez, Chamberlain & Wood, 2011; Hewett Ragheb & Walters, 2011; Kesler & Walters, 2012), we hypothesized increases in neighboring group sizes would have direct positive effects on the size of a given RCW group (h7). Additionally, considering RCWs are group-territorial and experience heightened competition where neighboring cluster density is high and neighboring group sizes are large (a proxy for intraspecific competition; Garabedian *et al.*, 2018), we hypothesized increases in neighboring group sizes and the associated intraspecific competition would have direct negative effects on fledgling production (h8). Given widespread positive group size effects on reproduction reported for RCWs (Walters *et al.*, 2002; Conner *et al.*, 2004; Garabedian *et al.*, 2017, 2019*c*) and other cooperatively breeding birds (Koenig, 1981; Brouwer *et al.*, 2009), we hypothesized group size would have direct positive effects on fledgling production (h9).

Indirect effects mediated by group size

Group size is typically described as directly and positively impacting reproduction for RCWs (James *et al.*, 1997, 2001; McKellar *et al.*, 2014). We built on this understanding by testing the hypothesis that group size would mediate a positive indirect effect of forest structure on fledgling production (h10).

Data acquisition and preparation

We obtained group sizes, fledgling production, and cluster locations in 2018, 2019, and 2020 for a sample of 63 RCW groups from SRS monitoring data (Fig. 3; we sampled the same 63 groups during each of the 3 years). Monitoring data consisted of records of group productivity and habitat management actions documented by U.S. Forest Service personnel during annual surveys conducted since 1985. Following U.S. Fish and Wildlife Service monitoring protocols (U.S. Fish and Wildlife Service, 2003), U.S. Forest Service personnel performed nest checks at each RCW cluster every 7–11 days during the breeding season (March–July) to document reproductive success (i.e. clutch size, nestling production, and fledgling production), and group size and composition (i.e. age and identity of group members). In addition to nest checks, U.S. Forest Service personnel annually document management actions applied to each RCW cluster (e.g. area treated prescribed fire, hardwood midstory control, artificial cavity installations). We used monitoring data from 2018, 2019, and 2020 to compile: (1) neighboring group sizes (i.e. calculated as the total number of individual RCWs occupying clusters within 800 m of a sampled RCW group, minus the number of individual RCWs in the sampled group); (2) group size; and (3) fledgling production during each of the 3 years for the 63 RCW groups. Given our hypotheses also involved carry-over effects (i.e. lagged effects) of woodpecker variables from the year prior to each of 2018, 2019, and 2020, we used monitoring data from 2017, 2018, and 2019 to calculate fledgling production and

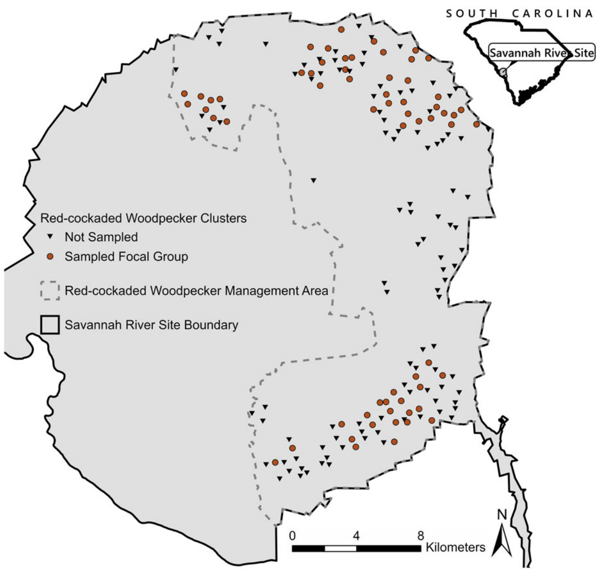

Figure 3 Distribution of red-cockaded woodpecker clusters used to develop a piecewise structural equation model of woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2020.

neighboring cluster density during the previous year (i.e. calculated as the total number of active RCW clusters within 800 m of a sampled RCW group in the previous year).

We summarized neighboring group sizes, neighboring cluster density, forest structure, and area treated with prescribed fire using an 800-m circular buffer centered on each sampled RCW group's cluster. We chose an 800-m buffer because this distance: (1) is recommended in the RCW recovery plan for allocating space to individual RCW groups when home-range data are unavailable (as in our study; U.S. Fish and Wildlife Service, 2003); (2) includes nesting sites and the majority, if not all, of foraging sites routinely used by individual RCW groups (Rosenberg & McKelvey, 1999; Garabedian *et al.*, 2018); (3) includes neighboring groups likely to interact with a given RCW group; and (4) includes the most likely destinations for dispersing RCWs (Engstrom & Mikusinski, 1998).

We obtained spatial coordinates for areas in RCW habitat treated with prescribed fire from SRS monitoring data (U.S. Forest Service, unpubl. data). We chose a maximum window of 5 years for fire return intervals because this time window reflects the historic range of fire return intervals on SRS (Kilgo & Blake, 2005). In addition, a 5-year window facilitated comparison of preliminary models fit to prescribed fire data spanning 1- to 5-year return intervals. We calculated the area (number of hectares) treated with prescribed fire during the 5 years prior to each of 2018, 2019, and 2020. For example, for RCW data collected in 2020, we summarized the area treated with prescribed fire between 2020 and 2016 starting with 2020 (i.e. the year RCW data were collected), past 2 years relative to 2020 (2019–2020), past 3 years (2018–2020), past 4 years (2017–2020), and past 5 years (2016–2020). We used this approach to summarize the area treated with prescribed fire for RCW demographic data collected in 2018, 2019, and 2020 (Supporting Information Table S2).

We used high-resolution LiDAR-derived estimates for density of pines ≥35.6 cm dbh (hereafter, large pines), basal area (BA; m^2 ha^{-1}) of hardwoods 7.6–22.9 cm dbh (hereafter, hardwood midstory), and percent hardwood canopy cover to characterize forest structure available to each group during 2018, 2019, and 2020. Discrete return airborne LiDAR used in this study were acquired with an average of 8 returns m^{-2} across SRS in March 2018 from a fixed-wing aircraft using a Leica ALS70-HP LiDAR system. The FUSION program was used to process and summarize LiDAR sensor data (McGaughey, 2019). Regression methods were then used to relate LiDAR sensor data to forest inventory plots (n = 477) distributed across the entire SRS. The resulting regressions were used to predict forest structural attributes included in the RCW recovery plan (U.S. Fish and Wildlife Service, 2003) and populate raster layers at 30-m resolution across the entire SRS (McGaughey, Strunk & Cooke, 2019).

Following Garabedian *et al.* (2017), we used site-specific thresholds for large pines (≥22 stems ha^{-1}), hardwood midstory (<1.4 m^2 ha^{-1} BA), and hardwood canopy cover (<6%). Using conditional rules, we enumerated 30-m raster cells that satisfied site-specific structural thresholds for large pines, hardwood midstory, and hardwood canopy cover. We limited the number of LiDAR-derived forest structure variables to large pines, hardwood midstory, and hardwood canopy cover because: (1) LiDAR does not effectively capture all forest attributes included in the U.S. Fish and Wildlife Service (2003) recovery plan (e.g. herbaceous understory cover and hardwood midstory height); (2) these variables capture forest structural conditions that have been linked to RCW resource selection on SRS and other populations (McKellar *et al.*, 2014; McKellar, Kesler & Walters, 2015; Garabedian *et al.*, 2017, 2019*b*,*c*); and (3) including additional LiDAR-derived forest structure variables would likely overparameterize models, given the sample size. We assumed forest structure did not change from 2018 to 2020, and therefore used the same forest structure data for each RCW group sampled in each of 2018, 2019, and 2020. We used the Zonal toolset in the Spatial Analyst toolbox in ArcGIS to extract the number of hectares treated with prescribed fire and the number of hectares that satisfied each structural threshold (ESRI, 2017).

Data analysis

Fire return interval selection

We conducted a preliminary analysis of area treated with prescribed fire within the past 1, 2, 3, 4, and 5 years to identify the fire return interval to include in the final piecewise SEM. Based on our conceptual path model, we fit separate linear mixed-effects models (LMM) for each response variable (i.e. group size and fledgling production) to estimate effects for area treated with prescribed fire in the past 1, 2, 3, 4, and 5 years relative to each year of RCW data (i.e. the past 1, 2, 3, 4, and, 5 years relative to 2018, 2019, and 2020). We fit each of the preliminary fire LMMs with group ID (n = 63) nested in year (n = 3) as random intercept terms to account for likely correlations inherent to repeated measurements of sampled RCW groups. Based on visual examination of scatter plots that indicated nonlinear effects of area treated with prescribed fire on group size and fledgling production, we fit preliminary fire LMMs with linear and quadratic terms. Finally, we fit each preliminary fire LMM with a spherical correlation structure to account for spatially correlated responses because RCW clusters typically exhibit a clustered distribution on the landscape. We tested assumptions of LMMs by visually examining: (1) normality of model residuals and random effects using quantile-quantile plots; and (2) patterns in model residuals relative to each model covariate (Zuur, Ieno & Elphick, 2010). We used second-order Akaike Information Criterion (AIC$_c$; Hurvich & Tsai, 1989; Burnham & Anderson, 2002) to compare preliminary linear and quadratic fire LMMs and retained the fire return interval with the lowest AIC$_c$ for each response for use in the final piecewise SEM.

Piecewise SEM

We developed a final piecewise SEM as a combination of two LMMs, reflecting hypothesized direct and indirect relationships among group size, neighboring group sizes, fledgling production, forest structure, neighboring cluster density, prescribed fire, and philopatry. We fit each LMM component model with the same random intercept terms and spherical correlation structure as in preliminary fire return interval models described above. We did not consider quadratic terms for predictors, other than area treated with prescribed fire, because scatterplots indicated only linear relationships. We considered direct and indirect effects statistically significant at $\alpha \leq 0.05$.

In the first component model, we estimated effects of fledglings produced by a group in the previous year, neighboring cluster density during the previous year, neighboring group sizes, forest structure, and area treated with prescribed fire on RCW group size, to test the hypothesis that increases in area satisfying structural thresholds (h1) and treated with prescribed fire (h3), improved demographic connectivity (h5), philopatry (h6), and neighboring group sizes (h7) would lead to larger group sizes. In the second component model, we estimated effects of group size, neighboring group sizes, forest structure, and area treated with prescribed fire on fledgling production, to test the hypothesis that: (1) increases in area satisfying structural thresholds would have no effect on fledgling production (h2); (2) increases in area treated with prescribed fire (h4) and increases in group size (h9) would have positive effects on fledgling production; and (3) increases in neighboring group sizes (h8; a proxy for intraspecific competition; Garabedian *et al.*, 2018) would have a negative effect on fledgling production. Finally, we used estimated effects from the second component model to calculate indirect effects to test the hypothesis that group size would mediate positive effects of forest structure on fledgling production that would offset negative effects of neighboring group sizes mediated by group size (h10).

We used a directed-separation test to evaluate fit of the final piecewise SEM and identify missing paths, or paths between variables that are supported by the data, but not included in the final piecewise SEM. For the directed-separation test, a probability $\leq$0.05 indicated the SEM was poorly supported by the data and further model refinement was required (e.g. adding missing paths to the piecewise SEM; Shipley, 2009). We used variance inflation factors (VIF) to test for multicollinearity in each component model (Neter, Wasserman & Kutner, 1985; Zuur *et al.*, 2010), and Moran's I to test for spatial autocorrelation in residuals of the fitted piecewise SEM across 30 distance bands ranging between 200 and 10 000 m. We tested assumptions of each component model by visually examining normality of residuals and random effects, and patterns in residuals relative to each model covariate as in preliminary fire return interval models described above. After assessing the overall fit of the final piecewise SEM, spatial autocorrelation, multicollinearity, and normality of residuals, we used 10 000 nonparametric bootstrap replicates to evaluate the effects of sample variation (e.g. removing a given RCW group from our dataset) on the consistency and statistical significance of direct and indirect effects. We reported R^2 for each component model, calculated following Nakagawa, Johnson & Schielzeth (2017). Finally, we used partial residual plots to visualize unique effects of predictors (i.e. controlling for effects of other predictors) included in each component model (Lefcheck, 2016). We conducted all analyses in the R Statistical Environment (R Core Team, 2020) using the contributed packages 'nlme' (Pinheiro *et al.*, 2020) to fit individual component models, 'piecewiseSEM' (Lefcheck, 2016) to fit component models in a piecewise SEM framework, 'pgirmess' (Giraudoux, 2018) to test for spatial autocorrelation of the fitted piecewise SEM residuals, and 'semEff' (Murphy, 2020) for calculation of bootstrapped direct and indirect effects.

Results

Mean group size, fledgling production, neighboring cluster density during the previous year, neighboring group sizes, fledglings produced during the previous year, and forest structure were comparable among RCW clusters sampled during each of 2018, 2019, and 2020 (i.e. means of variables were within 1 SD across years; Table 2).

We retained area treated with prescribed fire within the past 2 years as linear and quadratic terms in each component model of the final piecewise SEM (Table 3). The final piecewise SEM showed a good fit to the observed data (i.e. no missing paths; Fisher's C = 0.783, d.f. = 4, P = 0.94) and explained 55% of the variation in group size and 63% of the variation in fledgling production (Fig. 4). All predictors included in the final piecewise SEM had a VIF <3, indicating multicollinearity did not significantly bias results. Moran's I estimates were <|0.15| with P-values >0.05 across all distance bands tested, indicating no significant spatial autocorrelation in model residuals (Supporting Information Figure S1).

Table 2 Summary of variables used to develop a piecewise structural equation model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year)

Variable[a]	Year	Mean (SD)	Range
Group size	2018	3.1 (0.7)	2–4
	2019	2.9 (0.8)	2–4
	2020	3.1 (0.8)	2–4
Neighboring group sizes	2018	7.8 (3.6)	2–16
	2019	6.9 (3.6)	1–15
	2020	7.3 (2.9)	2–14
Fledgling production	2018	2.5 (0.8)	1–4
	2019	2.5 (0.7)	1–4
	2020	2.5 (0.7)	1–4
Fledglings$_{t-1}$	2018	2 (1.2)	0–4
	2019	1.7 (1.2)	0–4
	2020	2.2 (1)	0–4
Neighboring cluster density$_{t-1}$	2018	2.6 (1)	1–4
	2019	2.5 (1)	1–4
	2020	2.5 (1)	1–4
HA LP	2018	125.5 (28.1)	65.4–195.4
	2019	126.2 (32.6)	67.4–195.4
	2020	127.6 (29)	67.6–195.4
HA HWMID	2018	122.8 (27.8)	64.1–179.2
	2019	122.8 (27.8)	63.2–179.2
	2020	123.2 (28.7)	64.3–179.2
HA HWCOV	2018	56.3 (24.1)	6.1–103.5
	2019	56.3 (24.1)	6.1–103.5
	2020	56.7 (25)	6.2–103.5

Definitions for all variables are in Table 1.

[a] Definitions of variable abbreviations include: (1) $t - 1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover.

Residuals of each component model were normally distributed (Supporting Information Figure S2) and there were no patterns in relationships between residuals and model covariates (Supporting Information Figure S3), indicating distributional assumptions of LMMs were satisfied. Bootstrapped effect size estimates tended to be smaller than standardized effect estimates from standard model output, but direction of effects (i.e. positive or negative) did not differ (Table 4).

Forest structure

In agreement with our hypothesis (h1), area satisfying thresholds for large pines and hardwood midstory (but not hardwood canopy cover) had direct positive effects on group size (Table 4; Figs 4 and 5a). In agreement with our hypothesis (h2), area satisfying thresholds for large pines, hardwood midstory, and hardwood canopy cover did not affect fledgling production (Table 4; Figs 4 and 5b).

Prescribed fire

In partial agreement with our hypothesis (h3), the linear term for area treated with prescribed fire within the past 2 years had a direct positive effect on group size, whereas the quadratic term had no effect (Table 4; Figs 4 and 5a). In partial agreement with our hypothesis (h4), linear and quadratic terms for area treated with prescribed fire within the past 2 years had direct positive and negative effects, respectively, on fledgling production (Table 4; Figs 4 and 5b). However, the bootstrapped quadratic effect for area treated with prescribed fire within the past 2 years on fledgling production was not statistically significant (Table 4; Figs 4 and 5b).

Demographic connectivity and philopatry

Contrary to our hypothesis (h5), the number of neighboring clusters during the previous year had no effect on group size (Table 4; Figs 4 and 5a). In agreement with two of our hypotheses (h6 and h7), fledglings produced within a RCW group in the previous year and neighboring group sizes had a direct positive effects on group size (Table 4; Figs 4 and 5a,b).

Table 3 Bootstrapped standardized effect sizes, 95% confidence intervals, and model delta AIC$_c$ values (ΔAIC$_c$) for linear-mixed effects models of relationships between red-cockaded woodpecker (RCW) response variables (group size and fledgling production) and linear and quadratic terms for area (hectares) treated with prescribed fire within 800 m of RCW clusters during 1–5 year fire return intervals on Savannah River Site, South Carolina, USA in 2018, 2019, and 2020 (n = 63 during each year)

			Effect size (95% CI)	
Model response	Return interval	ΔAIC$_c$	Linear	Quadratic
Group size	1 year	22.1	0.021 (−0.039 to 0.106)	0.006 (−0.092 to 0.026)
	2 years	**0.0**	**0.145 (0.102 to 0.256)**	**−0.045 (−0.153 to 0.026)**
	3 years	7.1	0.138 (0.083 to 0.252)	−0.017 (−0.107 to 0.049)
	4 years	12.2	0.139 (0.080 to 0.259)	−0.137 (−0.266 to −0.062)
	5 years	14.7	0.126 (0.038 to 0.248)	−0.111 (−0.256 to −0.059)
Fledgling production	1 year	78.1	0.072 (−0.064 to 0.168)	−0.011 (−0.092 to 0.105)
	2 years	**0.0**	**0.395 (0.315 to 0.477)**	**−0.093 (−0.200 to −0.063)**
	3 years	36.5	0.350 (0.258 to 0.434)	−0.181 (−0.255 to −0.097)
	4 years	50.8	0.273 (0.185 to 0.370)	−0.161 (−0.268 to −0.063)
	5 years	61.5	0.229 (0.095 to 0.335)	−0.174 (−0.275 to −0.092)

Return intervals are relative to each year of woodpecker data described in Supporting Information Table S2. Top candidate models (i.e. ΔAIC$_c$ = 0) are denoted in bold.

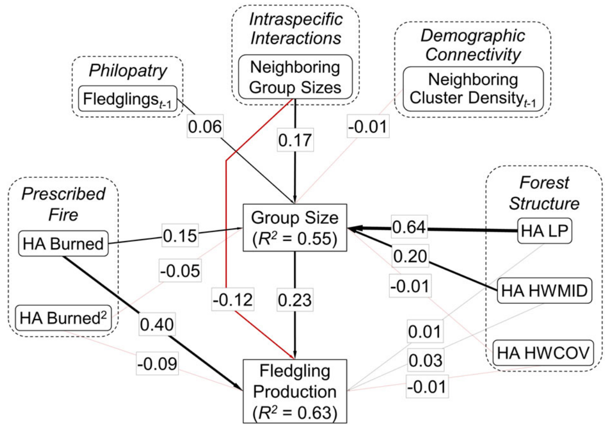

Figure 4 Path model illustrating the final piecewise structural equation model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year). Square boxes denote response variables for each component model and round boxes denote predictors, with arrows (i.e. paths) pointing from predictors to responses. Square boxes overlaying arrows denote bootstrapped standardized effect sizes. Transparent arrows indicate non-significant effects (bootstrapped 95% confidence intervals overlapped 0) and solid arrows represent significant effects (bootstrapped 95% confidence intervals did not overlap 0); width and color of lines reflects the magnitude and direction (positive = black, negative = red) of bootstrapped standardized effects. Definitions of variable abbreviations include: (1) $t-1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover. Definitions for all variables are in Table 1.

Neighboring group sizes and group size

In agreement with our hypothesis (h8), neighboring group sizes had a direct negative effect on fledgling production (Table 4; Figs 4 and 5a). In agreement with our hypothesis (h9), group size had a direct positive effect on fledgling production, which was larger than the direct negative effect of neighboring group sizes on fledgling production (Table 4; Figs 4 and 5b).

Indirect effects mediated by group size

In agreement with our hypothesis (h10), increased area satisfying thresholds for large pines and hardwood midstory (but not hardwood canopy cover) indirectly increased fledgling production via positive effects on group size (Table 5). Similarly, increased area treated with prescribed fire within the past 2 years and fledglings produced during the previous year indirectly increased fledgling production via positive effects on group size (Table 5). Interestingly, increased neighboring group sizes indirectly increased fledgling production via positive effects on group size, suggesting positive group size effects on fledgling production offset negative effects of neighboring group sizes (as described by h8; Table 5).

Discussion

Our results supported our hypothesis that group size mediates effects of forest structure and mitigates density-dependent declines in productivity in a recovering social woodpecker population. The overall benefits of ongoing habitat management, particularly as related to forest structure,

Table 4 Estimates of unstandardized direct effects with standard errors ($\beta \pm$ SE), standardized direct effects (β_{std}), and standardized bootstrapped direct effects with 95% confidence intervals ($\beta_{std.boot}$ [95% CI]) for predictors included in each component model (Response) included in the final piecewise structural equation model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year)

Response	Predictor[a]	$\beta \pm$ SE	β_{std}	$\beta_{std\cdot boot}$ (95% CI)
Group size	Fledglings$_{t-1}$	0.071 ± 0.03[b]	0.142[b]	0.058 (0.023 to 0.141)[b]
	Neighboring group sizes	0.059 ± 0.02[b]	0.440[b]	0.171 (0.063 to 0.310)[b]
	Neighboring cluster density$_{t-1}$	−0.059 ± 0.07	−0.089	−0.010 (−0.184 to 0.109)
	HA LP	0.127 ± 0.02[b]	0.992[b]	0.640 (0.532 to 0.641)[b]
	HA HWMID	0.067 ± 0.02[b]	0.399[b]	0.198 (0.035 to 0.323)[b]
	HA HWCOV	0.007 ± 0.03	−0.003	−0.011 (−0.188 to 0.180)
	HA burned	0.066 ± 0.02[b]	0.659[b]	0.145 (0.099 to 0.223)[b]
	HA burned^2	−0.002 ± 0.002	−0.185	−0.045 (−0.133 to 0.028)
Fledgling production	Group size	0.333 ± 0.07[b]	0.222[b]	0.230 (0.141 to 0.331)[b]
	Neighboring group sizes	−0.031 ± 0.01[b]	−0.157[b]	−0.119 (−0.197 to −0.040)[b]
	HA LP	0.003 ± 0.02	0.018	0.010 (−0.070 to 0.092)
	HA HWMID	0.012 ± 0.02	0.047	0.027 (−0.050 to 0.099)
	HA HWCOV	−0.006 ± 0.02	−0.019	−0.011 (−0.079 to 0.061)
	HA burned	0.124 ± 0.01[b]	0.829[b]	0.395 (0.306 to 0.459)[b]
	HA burned^2	−0.003 ± 0.001[b]	−0.230[b]	−0.093 (−0.194 to −0.016)

Definitions for all variables are in Table 1.

[a] Definitions of variable abbreviations include: (1) $t-1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover.

[b] 95% bootstrapped confidence intervals that did not overlap 0.

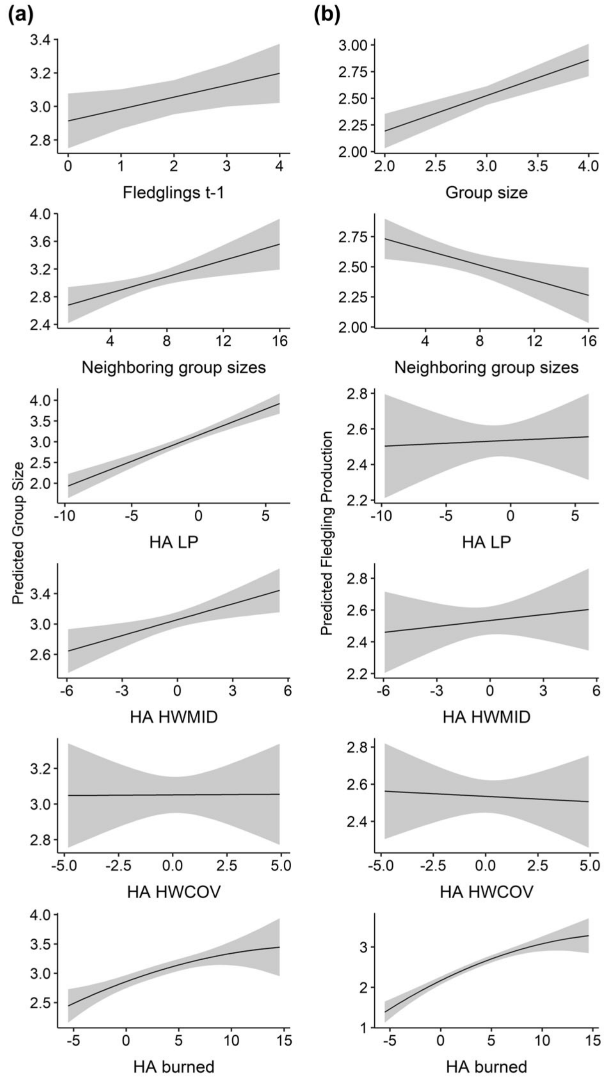

Figure 5 Partial residual plots illustrating unique direct effects and 95% confidence intervals (lines and gray shaded areas, respectively) for predictors included in group size (a) and fledgling production (b) component models of the piecewise structural equation model of red-cockaded woodpecker productivity on Savannah River Site, SC, USA, in 2018, 2019, and 2020 (n = 63 during each year). Definitions of variable abbreviations include: (1) $t - 1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover. Definitions for all variables are in Table 1.

to RCW populations primarily can be explained by direct positive effects of forest structure on group sizes that indirectly lead to greater fledgling production. Walters *et al.* (2002) highlighted the possibility group size may mediate indirect effects of forest structure on fledgling production and our study provides evidence supporting this indirect relationship. We showed that forest structure did not directly influence RCW fledgling production, which contrasts with earlier studies that suggested improvements to forest structure directly improves reproductive success (Hardesty, Gault & Percival, 1997; James *et al*., 1997, 2001; Davenport *et al*., 2000; Ramirez & Ober, 2014). Many earlier studies of RCW habitat-fitness relationships did not control for simultaneous effects of group size or intraspecific competition (James *et al*., 1997, 2001; Butler & Tappe, 2008; McKellar *et al*., 2014; Ramirez & Ober, 2014). Our results indicate not controlling for these effects may have artificially inflated effects of forest structure on fledgling production. Indeed, the positive effects of RCW group size on reproductive success have been shown to be relatively more important than effects of forest structure in RCWs (Garabedian *et al*., 2017, 2019*a*,*c*) and other cooperatively breeding birds (Doerr & Doerr, 2007). Greater resource demands of larger groups may explain why forest structure had direct positive effects on group sizes, but not fledgling production. Groups on high-quality territories (as defined by forest structure) may also be in better physical condition than groups on relatively low-quality territories (Kappes, 2008), thereby reducing costs of territorial defense that can reduce fledgling production (Garabedian *et al*., 2018). Thus, higher quality territories indirectly improve fledgling production by supporting larger groups, and larger groups in turn have direct positive effects on fledgling production that offset negative effects of competition with neighboring groups under high-density conditions.

The positive effects of area treated with prescribed fire on multiple aspects of woodpecker productivity could be due to direct or indirect effects of fire on arthropod prey. Previous research has suggested fire indirectly improves RCW productivity via increased herbaceous ground cover and nutrient cycling that increases abundance and nutritive value of arthropod prey, which in turn improves RCW productivity (James *et al*., 1997). Prescribed fire provides an influx of nutrients to the forest floor, which has been linked to short-term increases in N and P availability in soil (Butnor *et al*., 2020) and herbaceous understory plants (Lavoie *et al*., 2010). Although some studies have linked arthropod nutritive value to avian prey selection (Razeng & Watson, 2015), whether the short-term increase in concentrations of nutrients in herbaceous groundcover following prescribed fire leads to measureable increases in nutritive value of arthropod prey is not well-supported in published research. Studies on relationships among arthropods, fire, and herbaceous groundcover in southern pine forests have produced mixed results. Some studies suggest arthropod abundance and biomass increase with greater herbaceous groundcover, but not nutrients in foliage and soil (Conner, Saenz & Burt, 2006), whereas others suggest arthropod abundance and biomass do not increase with greater herbaceous groundcover following prescribed fire (Hanula, Franzreb & Pepper, 2000; Hanula & Horn, 2004).

Our results indicate that the benefits of prescribed fire extend to more than just maintenance of specific forest conditions, highlighting the importance of differences in outcomes from different management interventions used as surrogates for disturbance processes like prescribed fire. Although canopy thinning, mechanical hardwood midstory reduction, and prescribed fire can be used to maintain similar

Table 5 Bootstrapped estimates of indirect effects mediated by group size on fledgling production of red-cockaded woodpeckers on Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year)

Indirect path[b]	Indirect effect
HA burned → Group size → Fledgling production	0.033 (0.023 to 0.067)[b]
HA burned^2 → Group size → Fledgling production	−0.010 (−0.035 to 0.015)
HA LP → Group size → Fledgling production	0.147 (0.053 to 0.186)[b]
HA HWMID → Group size → Fledgling production	0.044 (0.002 to 0.095)[b]
HA HWCOV → Group size → Fledgling production	−0.003 (−0.047 to 0.049)
Neighboring cluster density$_{t-1}$ → Group size → Fledgling production	−0.002 (−0.038 to 0.025)
Fledglings$_{t-1}$ → Group size → Fledgling production	0.013 (0.004 to 0.038)[b]
Neighboring group sizes → Group size → Fledgling production	0.039 (0.016 to 0.089)[b]

Definitions for all variables are in Table 1.

[a] Definitions of variable abbreviations include: (1) $t-1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover.

[b] Bootstrapped 95% confidence intervals that did not overlap 0.

forest conditions, benefits to bark-foraging birds like RCW are enhanced when canopy thinning and mechanical hardwood midstory reduction are followed by prescribed fire (Fontaine & Kennedy, 2012). In other fire-prone forests, different disturbances (e.g. wildfire, low-intensity prescribed fire, and bark-beetle outbreaks) are associated with different arthropod prey bases, and low-intensity prescribed fire is most likely to increase availability of preferred prey for several woodpeckers (Nappi et al., 2010). Foraging success in black-backed woodpeckers *Picoides arcticus*, for example, increases following severe fire due to increased availability of preferred arthropod prey (Rota et al., 2015). Similarly, arthropods available to bark-foraging birds in southern pine forests frequently move from the understory onto pine boles (Hanula & Franzreb, 1998), and low-intensity prescribed fire may stimulate this type of vertical movement of RCW arthropod prey (Dell et al., 2017) thereby increasing foraging success. Our finding that area treated with prescribed fire within the past 2 years had direct positive effects on RCWs aligns with several studies on cavity-nesting and bark-foraging birds that found fire effects on bird productivity were related to direct effects of chemical cues that attracted preferred arthropod prey to burned areas, independent of direct effects of fire on forest structure (Lyons et al., 2008; Nappi & Drapeau, 2009; Russell et al., 2009). However, fire regimes that mimic the variability in frequency and extent of low-intensity fires may provide the overall greatest benefit to conservation of wildlife in fire-prone forests (Lashley et al., 2014; Darracq, Boone & McCleery, 2016).

When availability of limiting resources changes through time due to changes in population density or group sizes, the relative benefits of demographic connectivity may also change. Contrary to our hypothesis and recent research (Garabedian et al., 2019*a*), neighboring cluster density during the previous year did not have an effect on group size. Assuming forest structure was similar across sampled clusters, the absence of this effect on group size does not necessarily indicate a lack of benefits associated with demographic connectivity (e.g. improved dispersal success, breeder replacement), but rather may be related to cavity availability and number of cavity competitors. Cavity competition can be intense in RCW clusters with few or no surplus cavities. This competitive environment may preclude dispersing juveniles from joining a neighboring group (Pasinelli & Walters, 2002), and force them to incur greater risks associated with long-distance dispersal (Kesler, Walters & Kappes, 2010) or becoming a floater (Walters, 1990). If a lack of surplus cavities did force RCWs to disperse longer distances during the 3 years of data used in our study, the lack of effect of neighboring cluster density during the previous year could be because the 800-m buffer distance did not capture sufficient dispersal destinations.

By simultaneously accounting for direct and indirect drivers of productivity in social wildlife using SEM, our study contributes to the understanding of how recovery of social wildlife populations and concomitant increases in population sizes can alter previously documented habitat-fitness relationships. Although early RCW research highlighted the importance of forest structure to group productivity, our SEM approach indicates prescribed fire, group size, and neighboring group sizes will gain importance relative to forest structure as high-density conditions become more common. In contrast to assuming all predictors have direct effects on species' responses, the SEM framework allowed us to parse direct effects of fire, group size, and neighboring group sizes from indirect effects of forest structure on fledgling production. Had we not simultaneously modeled effects of forest structure and area treated with prescribed fire in each component SEM model, we may have erroneously concluded forest management provides limited benefit to RCW fledgling production. Rather, we showed that where baseline forest structural conditions are satisfied, area treated with prescribed fire had positive direct and indirect effects on group size and fledgling production.

Adaptive management of threatened and endangered social wildlife in fire-prone systems requires an understanding of complex relationships among multiple variables and ecological processes. By leveraging multiple metrics related to productivity in an analytical framework allowing inference on direct and indirect effects, we were able to evaluate the extent to which group size mediated effects of forest structure on RCW productivity. Ongoing forest management and frequent fire return intervals will promote larger group sizes that in turn improve fledgling production and simultaneously offset costs of intraspecific competition under high-density conditions. Considering area treated with prescribed fire within the past 2 years had positive direct and indirect effects on group size and fledgling production after controlling for forest structure, our study highlights the importance of maintaining frequent fire return intervals in southern pine forests for wildlife conservation. With ongoing management and increases in area of forest that satisfies a set of minimal structural conditions, our study indicates ongoing use of frequent prescribed fire will gain importance to long-term viability and productivity of RCWs and likely other conservation-reliant species in fire-maintained southern pine forests. Our results indicate 2–3 year fire return intervals are ideal for maximizing RCW productivity on SRS, although alternative intervals may be more effective for other RCW populations due to geographic variation in soils, climate, and forest conditions (McKellar *et al*., 2014). Given the dramatic growth of RCW populations across the species' range and potential for down-listing, and by extension reduced management requirements, our study provides an understanding of how recovered populations may respond to changes in management intensity, particularly reduced prescribed fire return intervals, over the long-term.

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Conflict of interest

The authors declare no conflicts of interest.

Data availability statement

Data are archived in the Figshare Repository https://doi.org/10.6084/m9.figshare.17018753.v1

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Moran's *I* estimates assessing spatial autocorrelation in a piecewise structural equation model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year).

Figure S2. Quantile-quantile plots of residuals from component models for group size (a) and fledgling production (b) developed as a piecewise structural equation model of red-cockaded woodpecker productivity on Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year).

Figure S3. Scatter plots illustrating distribution of residuals from piecwise structural equation component models for group size (a) and fledgling production (b) relative to covariates in each component model of red-cockaded woodpecker productivity on Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year). Definitions of variable abbreviations include: (1) $t - 1$ = 1 year prior to current year (current year = 2018, 2019, and 2020); (2) HA = hectare; (3) LP = large pines; (4) HWMID = hardwood midstory; (5) HWCOV = hardwood canopy cover. Definitions for all variables are in Table 1.

Table S1. Overview and justification for *a priori* hypothesized relationships used to develop a piecewise structural equation model of red-cockaded woodpecker productivity on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year).

Table S2. Summary of mean (SD), range, total, and percent of area (hectares) treated with prescribed fire within 800 m of red-cockaded woodpecker clusters included in the piecewise structural equation model of woodpecker productivity during 1–5 year fire return intervals on the Savannah River Site, South Carolina, USA, in 2018, 2019, and 2020 (n = 63 during each year).