

Effects of group size and group density on trade-offs in resource selection by a group-territorial central-place foraging woodpecker

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Trade-offs in resource selection by central-place foragers are driven by the need to balance the benefits of selecting resources against the costs of travel from the central place. For group-territorial central-place foraging birds, trade-offs in resource selection are likely to be complicated by a competitive advantage for larger groups at high group density that may limit accessibility of high-quality distant resources to small groups. We used the group-territorial, central-place foraging Red-cockaded Woodpecker *Leuconotopicus borealis* (RCW) as a case study to test predictions that increases in group density lead to differences in foraging distances and resource selection for groups of different sizes. We used GPS tracking and LiDAR-derived habitat data to model effects of group size on foraging distances and selection for high-quality pines (≥ 35.6 cm diameter at breast height (dbh)) and lower quality pines (25.4–35.6 cm dbh) by RCW groups across low ($n = 14$), moderate ($n = 10$) and high group density ($n = 10$) conditions. At low and moderate group density, all RCW groups selected distant high-quality pines in addition to those near the central place because competition for resources was low. In contrast, at high group density, larger groups travelled further to select high-quality pines, whereas smaller groups selected high-quality pines only when they were close to the central place and, conversely, were more likely to select lower quality pines at greater distances from the central place. Selection for high-quality pines only when close to the cavity tree cluster at high group density is important to long-term fitness of small RCW groups because it allows them to maximize benefits from both territorial defence and selecting high-quality resources while minimizing costs of competition. These relationships suggest that intraspecific competition at high group density entails substantive costs to smaller groups of territorial central-place foragers by limiting accessibility of distant high-quality foraging resources.

Keywords: competition, density dependence, endangered species, forest structure, functional response, LiDAR, Red-cockaded Woodpecker, space use.

Resource selection is a dynamic process wherein animals maximize fitness through complex trade-offs with the resources they use (MacArthur & Pianka 1966, Schoener 1971, Myserud & Ims 1998). Trade-offs in resource selection are especially relevant for central-place foragers because they must balance the benefits of selecting

resources against costs of travel from the central place (Orians & Pearson 1979). Distance is a main determinant of the costs and benefits of selecting resources for central-place foragers (Olsson *et al.* 2008). In many cases, central-place foraging birds travelling greater distances will select higher-quality resources and provision nests with large prey that have high nutritional value (Caraco *et al.* 1980, Martindale 1983). When making shorter foraging trips, central-place foraging birds are more likely to select lower-quality resources and provision nests

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with smaller prey of lower nutritional value (Cut-hill & Kacelnik 1990).

Among group-territorial central-place foragers, group size and group density affect resource selection by allowing larger groups to exclude smaller groups from distant, high-quality resources. Costs of travel may be lower for larger groups of central-place foragers because they typically outcompete and displace smaller foraging groups from access to distant, high-quality forage resources (Pereira *et al.* 2003). This may lead to greater foraging distances for larger groups of central-place foragers than for smaller groups that remain close to the central place to avoid costly competitive interactions (Ydenberg *et al.* 1986). Small groups may reduce foraging distances at high group density due to high costs of competing with larger neighbouring groups for access to high-quality resources (Martindale 1982). Increases in group density that limit accessibility of distant resources may cause smaller groups of territorial central-place foragers to adjust foraging distances and select different resources rather than competing with neighbouring groups for access to distant resources (Brown 2000).

A competitive advantage of larger groups may force smaller groups to select only uncontested or easily defensible resources close to the central place when group density is high. At low group density, groups of any size should be able to select resources that provide the greatest benefit to fitness because intraspecific competition for resources is low (Wiens 1973). At high group density, relatively large groups of territorial central-place foragers may have a competitive advantage that reduces the need to trade-off selection for high-quality distant resources with territorial defence (Rozen-Rechels *et al.* 2015). In larger groups of cooperatively breeding birds, for example, some group members may travel to forage on high-quality resources while others stay to defend the nest-site (Martindale 1982). Larger groups may therefore be able to travel greater distances to forage at high group density because some group members offset costs by remaining close to the central place for territorial defence (Ligon & Ligon 1978). In contrast, smaller groups may not have the same competitive advantage at high group density, and therefore may only be able to forage on high-quality resources if they are closer to the nest-site where they can reduce costs of travel and competition (Lameris *et al.* 2018). Hence, at high group density, smaller groups may be more likely to be

restricted to relatively low-quality resources when foraging farther from the central place (Ydenberg *et al.* 1986). In social species, exploitation of relatively low-quality resources farther from the central place may still allow smaller groups to gain information on neighbouring groups that provide offsetting, indirect long-term benefits of demographic connectivity (Greene & Stamps 2001). Despite the importance of group density and size for group-territorial, central-place foragers established in previous research, joint effects of group density and size on foraging costs remain poorly understood.

In this study, we investigated whether increases in group density altered travel costs and led to differences in resource selection among different group sizes in the group-territorial, central-place foraging Red-cockaded Woodpecker *Leuconotopicus borealis* (RCW). The RCW provides a good case study because resource selection by foraging RCWs is driven simultaneously by forest structure (Walters *et al.* 2002), distance from cavity tree clusters (Rosenberg & McKelvey 1999), group size (McKellar *et al.* 2016) and neighbouring group density (DeLotelle *et al.* 1987, Garabedian *et al.* 2018b). The RCW is a cooperatively breeding species that lives in social groups with a breeding pair and up to five helper individuals (Walters *et al.* 1992). Foraging RCWs consistently select the largest and oldest available pines *Pinus* spp. (Engstrom & Sanders 1997, Zwicker & Walters 1999). Selection for the largest and oldest pines has been linked to improved group fitness (Walters *et al.* 2002), probably due to greater biomass and abundance of arthropod prey available on large pines than on smaller pines (Hanula *et al.* 2000a). Group-level productivity also tends to be greater in larger groups than in smaller groups because of the presence of helpers that assist with foraging, territorial defence, cavity excavation and maintenance, incubation and nest provisioning (Conner *et al.* 2001, 2004).

Studies addressing the relationship between group size and travel distances have produced mixed results, some suggesting that larger groups travel greater distances from cavity tree clusters (i.e. the aggregate of cavity trees defended and occupied by an RCW group) to forage on higher-quality large pines (McKellar *et al.* 2016), whereas others found that they did not travel greater distances (Franzreb 2004, 2006). Yet, whether increases in group density alter travel costs and lead to these observed differences in resource

selection among groups of different sizes is unknown (U.S. Fish and Wildlife Service (USFWS) 2003, Garabedian *et al.* 2014a).

Our objective was to compare effects of distance on selection for specific pine size classes by foraging RCW groups of different sizes across three group density conditions, to determine whether differences in selection between pine size classes at different distances are driven by interactions between group size and group density. Accordingly, we tested five predictions. At low and moderate group density, we predicted that all RCW groups would select for pines ≥ 35.6 cm diameter at breast height (dbh) (hereafter, large pines) at greater distances because access to foraging habitat is not constrained by neighbouring groups and competition for resources is low (prediction 1; Hooper *et al.* 1982, Garabedian *et al.* 2018a). At high group density, we predicted that larger RCW groups would select for large pines at greater distances because they are more likely to outcompete smaller groups for access to high-quality resources in shared foraging habitat (prediction 2; Hooper *et al.* 1982, DeLotelle *et al.* 1987). Conversely, at high group density we predicted that smaller RCW groups would select for large pines only close to the cavity tree cluster to compensate for restricted access to distant large pines (prediction 3; Franzreb 2004, 2006). Additionally, at high group density we predicted that selection for smaller pines of 25.4–35.6 cm dbh (hereafter, medium pines) would not change with distance for larger groups because they are more likely to monopolize distant high-quality large pines (prediction 4) but would do so for smaller groups that are restricted by competition from larger foraging groups for access to large pines (prediction 5).

METHODS

Study site

We conducted the study on the U.S. Department of Energy's Savannah River Site (SRS), South Carolina, USA. The SRS is characterized by sandy soils and gently sloping hills dominated by pines *Pinus* spp., with scattered hardwoods (Kilgo & Blake 2005). Prior to federal acquisition in 1951, most of the SRS was maintained as agricultural fields or more recently had been harvested for timber (White 2005). The U.S. Department of Agriculture Forest Service has managed the natural

resources on the SRS since 1952 and reforested most of the site (Imm & McLeod 2005). Approximately 53 014 ha of the SRS was re-forested with artificially regenerated stands of loblolly *Pinus taeda*, longleaf *Pinus palustris* and slash *Pinus elliotii* pines with an additional 2832 ha with pine–hardwood mixtures. The remaining 27 000 ha of forested area on the SRS includes bottomland hardwoods, forested wetlands/riparian areas and mixed-hardwood stands. Mixed pine–hardwood stands on the SRS typically include a mixture of longleaf pine, loblolly pine and *Quercus* spp. Mid-storey trees that reach the sub-canopy typically are small *Quercus* spp., but include sand hickory *Carya pallida*, sweetgum *Liquidambar styraciflua* and sassafras *Sassafras albidum*.

In conjunction with the Department of Energy, the U.S. Department of Agriculture Forest Service began management for RCWs in 1984 with the objective of restoring a viable population on the SRS. Under intensive management since 1985, the RCW population grew from three clusters with a combined total of four birds (Johnston 2005) to 103 clusters with a combined total of over 250 birds in 2018 (T. Mims pers. comm.). Management of RCW habitat on the SRS included prescribed fire and mechanical methods to limit mid-storey encroachment by hardwoods, construction of RCW recruitment clusters (i.e. an aggregate of more than four artificial cavities installed in unoccupied foraging habitat; USFWS 2003) to alleviate cavity tree limitations, and protection of the largest and oldest available pines (Allen *et al.* 1993, Haig *et al.* 1993, Franzreb 1997). As part of ongoing monitoring, U.S. 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 and group size for each cluster (USFWS 2003). All RCWs at the SRS have been uniquely colour-banded by U.S. Forest Service personnel.

Group density conditions

We used areas of RCW Thiessen habitat partitions (Lipscomb & Williams 1995) to calculate average group density for three aggregates of 10–14 neighbouring groups. We calculated group density as the total number of groups within a given aggregate divided by the total area delineated by the groups' Thiessen habitat partitions. Thiessen habitat partitions are 800-m-radius circular buffers

(~ 200 ha) centred on RCW cavity tree clusters, and have traditionally have been used to delineate foraging habitat for individual RCW groups. When clusters are < 800 m apart, Thiessen polygons are used to divide the total area of overlapping partitions equally based on distance between neighbouring clusters (USFWS 2003). Thus, RCW Thiessen habitat partitions are truncated as the density of neighbouring clusters increases (Schlicht *et al.* 2014). Further, our approach reflects the overall spatial neighbourhood that RCWs are likely to encounter when interacting with neighbouring groups and dispersing (Engstrom & Mikusinski 1998) and captures density-dependent changes in territorial behaviours (Garabedian *et al.* 2018a). Following Garabedian *et al.* (2018a), we used ranges of 0.25–0.50, 0.51–1.00 and ≥ 1.00 groups/50 ha to represent low, moderate and high group density conditions, respectively. The 50-ha denominator was selected to approximate the recommended minimum amount of good-quality foraging habitat allocated to individual RCW groups (USFWS 2003). Group density estimates for low- ($n = 14$), moderate- ($n = 10$) and high-density ($n = 10$) conditions in our study were approximately 0.42 groups/50 ha (or one group/~ 120 ha), 0.58 groups/50 ha (or one group/~ 85 ha) and 0.77 groups/50 ha (or one group/~ 65 ha), respectively.

Field methods

We used movement data to define resource availability for individual RCW groups across low-, moderate- and high-group density conditions (Fig. 1). We tracked individual RCW groups over a 4- to 8-h period (hereafter, 'follows'), recording location fixes using handheld GPS units (location accuracy of ± 3 m) at 15-min intervals (Franzreb 2006), twice a month between April 2014 and March 2015. In addition to location fixes, we also documented basic behaviours (e.g. foraging, resting, cavity work, feeding nestlings, agonistic territorial interactions among neighbouring RCW groups) at each 15-min interval. We targeted a 4- to 8-h range for 'follows' based on previous research indicating that this duration provides unbiased representations of RCW home-ranges (Hooper & Harlow 1986, Porter & Labisky 1986). Follows consisted of sustained visual contact with an RCW group beginning when individuals left their roosts in the morning and continuing until

contact with the group was lost, or until terminated due to inclement weather or management activities that precluded site access (e.g. prescribed burning). We recorded ≥ 15 location fixes throughout the day during each follow, thus providing ≥ 30 relocations per month. We considered follows to be incomplete if we recorded < 15 location fixes throughout a single day and repeated incomplete follows later in the same month. Although RCW group members typically forage as a cohesive unit, even concurrently in the same tree, we used location fixes for the breeding male of each sample group to represent movement of the entire group. We used spotting scopes to identify unique colour-band combinations to ensure that the breeding male was followed for each group.

LiDAR-derived habitat covariates

Following Garabedian *et al.* (2014b), we used LiDAR-derived estimates for density (stems/ha) of large pines (≥ 35.6 cm dbh), medium pines (25.4–35.6 cm dbh) and all hardwoods (≥ 7.6 cm dbh) to characterize foraging habitat available to individual RCW groups. Garabedian *et al.* (2014b) used regression methods to relate the LiDAR sensor data to forest inventory measurements collected across a range of forest conditions on the SRS. They used the resulting regressions to predict forest structural attributes included in the RCW recovery plan (USFWS 2003) and populate raster layers at 20-m resolution across the entire SRS. An 80-m grain size was optimal for characterizing foraging habitat quality based on their objective to minimize prediction error and maintain a grain size concordant with recommended methods for assessment and management of RCW foraging habitat (Garabedian *et al.* 2014b). Accordingly, we maintained the 80-m grain size for each LiDAR-derived habitat attribute.

Data analysis

Home-range estimation

We estimated fixed-kernel utilization distributions using the reference bandwidth (UDs; Worton 1989) with all group-specific foraging locations collected during follows to delineate home-range boundaries and resources available to individual RCW groups (type III design; Thomas & Taylor 2006). We estimated separate UD for each RCW

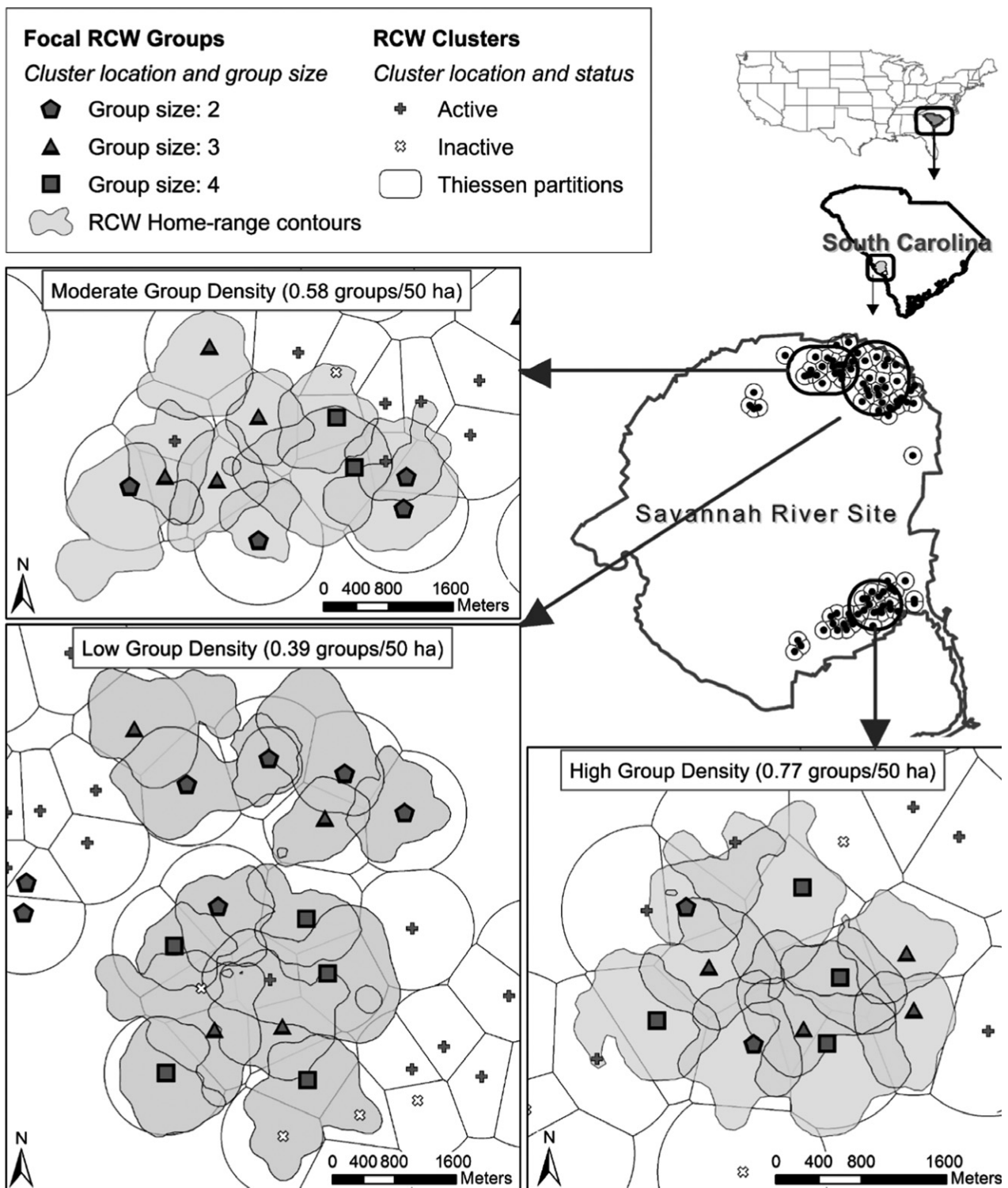


Figure 1. The spatial distribution and status of Red-cockaded Woodpecker cavity tree clusters and sample groups in high, moderate and low group density conditions on the Savannah River Site, South Carolina, USA, in 2014.

group on the same spatial grid used for the LiDAR-derived habitat data and considered all 80-m pixels within 99% UD contours as available to a given RCW group (the home-range). Next, we created a covariate for the Euclidean distance (m) to the centroid of each group's cavity tree clusters from the centre of individual pixels within 99% UD contours of each RCW group to account for effects of distance on selection (Rosenberg & McKelvey 1999). Prior to modelling, we scaled all LiDAR and distance covariates by dividing by the standard deviation of each covariate to improve model convergence (Zuur *et al.* 2009). Pearson correlation coefficients among all potential covariates were ≤ 0.60 , indicating no collinearity. We used the Neighborhood and Extraction toolsets in the Spatial Analyst toolbox in ArcGIS (ESRI 2017) to create a spatially explicit dataset for use in subsequent resource selection models. We used the Neighborhood toolset to count the number of foraging locations in each 80-m pixel within home-range of each RCW group, and subsequently used the Extraction toolset to spatially join counts of foraging locations with distance and LiDAR covariates.

Resource selection models

We modelled third-order (within home-ranges; Johnson 1980) resource selection using negative binomial generalized linear mixed-effects models (Zuur *et al.* 2009). We selected a negative binomial error distribution to account for overdispersion in observed counts of foraging locations for each RCW group (Hilbe 2011). We used RCW group home-ranges as replicates and fit group-specific counts of RCW foraging locations within individual pixels of each RCW home-range as the response variable and the log of total locations for each RCW group as an offset term to transform the observed number of RCW locations within each pixel to relative probability of use (Nielson & Sawyer 2013). Scaled LiDAR-derived habitat covariates, scaled distance from the cavity tree cluster, group size and group density were fitted as covariate predictors, and group density was fitted as a blocking factor to test for any coarser scale of group density in addition to that of finer scale distance effects (Møbæk *et al.* 2009, McLoughlin *et al.* 2010). We fit scaled LiDAR-derived large pines/ha and RCW group home-range sizes as random slope and intercept terms, respectively, to allow inference about how selection for large pines

varies among individual RCW groups relative to average selection for large pines for the entire RCW sample, and to determine how individual foraging RCW groups adjust selection conditional on home-range sizes (Gillies *et al.* 2006, Schielzeth & Forstmeier 2009). Additionally, fitting these random slope and intercept terms accounted for unbalanced sample sizes and non-independence of observations within individual RCW home-ranges (Schielzeth & Forstmeier 2009).

We developed five candidate resource selection models that included: (1) a null model that included only distance from the central place; (2) a distance-habitat interaction model; (3) a group size-distance-habitat interaction model; (4) a group density-distance-habitat interaction model; and (5) a group density-group size-distance-habitat interaction model. Candidate models included interactions among habitat covariates, distance, group size and/or group density to explicitly account for potential movement constraints, spatial autocorrelation and intraspecific competition that may confound estimates of selection for territorial central-place foragers (Rosenberg & McKelvey 1999, Matthiopoulos 2003, Rozen-Rechels *et al.* 2015).

We used estimated marginal mean contrasts to address each of our five predictions about how increases in group density led to differences in selection among groups of different sizes. We tested predictions 1, 2 and 3 by comparing effects of distance on selection for large pines, and predictions 4 and 5 by comparing effects of distance on selection for medium pines. Model convergence issues precluded fitting group size as a categorical variable; we therefore fit group size as an integer covariate in all models. Because there were no group sizes of 5 in low and moderate group density conditions, we pooled data for group sizes of ≥ 4 ($n = 4$) in the high group density condition to maintain balanced group size samples across group density conditions and improve model fit (Harrell 2013).

Model selection and evaluation

We used Akaike's criterion corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), Δ AIC_c and AIC_c weights for model selection (Burnham & Anderson 2002). We considered models with Δ AIC_c < 2 competitive candidate models. We used non-parametric bootstrapping techniques to evaluate precision of estimated coefficients in the

top supported resource selection model (Fox *et al.* 2015). We sampled with replacement to generate 500 bootstrap samples from the observed resource selection dataset and subsequently calculated bootstrapped coefficients and 95% confidence intervals for the best supported model. As needed for non-parametric bootstrapping techniques, we resampled observations from within individual RCW groups in each group density condition to maintain the grouping structure of the observed resource selection dataset (Fox *et al.* 2015). We conducted a retrospective power analysis by simulation ($n_{\text{simulations}} = 1000$) to determine whether small sample sizes within density conditions biased results (Bolker 2008). Finally, we tested model residuals for spatial autocorrelation using Moran's I statistic calculated at 23 distance bands ranging between 100 and 5000 m (Dormann *et al.* 2007). We conducted home-range and resource selection analyses in R (R Core Team 2019), using the packages *adehabitatHR* for home-range estimation (Calenge 2006), *lme4* for negative binomial mixed-effects models (Bates *et al.* 2015), *simr* for power analysis (Green & MacLeod 2016), *sjstats* for bootstrapping (Lüdtke 2019), *ncf* for testing model residuals for spatial autocorrelation (Bjornstad 2019) and *emmeans* for estimated marginal mean contrasts (Lenth 2019). We report all results as mean $\pm$ sd unless otherwise noted.

RESULTS

Home-range estimation

We collected 12 564 locations, representing six behaviours, for 34 RCW groups between April 2014 and March 2015 (Table S1). Foraging and nestling or fledgling provisioning behaviours were the most frequent and infrequent observations, respectively, across group density conditions (Table S1). The frequency of territorial interactions among neighbouring RCW groups tended to increase with group density (Table S1). The number of foraging locations used to estimate UD delineating RCW group home-ranges and available resources averaged 351, ranging from 191 to 437. The reference bandwidths used to estimate UD for each woodpecker group averaged 81 m, ranging from 44 to 125 m. The number of foraging locations within UD pixels averaged 5, ranging from 0 to 93. The number of pixels within RCW UD averaged 235, ranging from 81 to 354.

Group sizes averaged 2.8 ± 0.8 for the entire sample of RCW groups (Table 1). Overall, clutch size and fledgling production tended to be greatest in the largest groups (Table 1). Average home-range size (99% UD) for the entire sample of RCW groups was 150.8 ± 54.6 ha. Overall pine and hardwood densities within home-ranges in each group density condition were comparable (Table 1). Groups of two tended to have the smallest home-ranges within group density conditions, but there was no clear relationship between group size and home-range size across group density conditions (Table 1). Group size tended to increase with greater average density of large and medium pines within RCW home-ranges, and decrease with greater average density of hardwoods ≥ 7.6 cm dbh within home-ranges (Table 1).

Resource selection models

The best supported candidate resource selection model indicated differences in selection for specific pine size classes were driven by interactions between group size and group density (Table 2). The four-way interaction among group density, group size, distance and LiDAR-derived pine size classes had a significant effect on resource selection by foraging RCW groups (Table 3). Confidence intervals based on bootstrapping typically were more precise and revealed additional significant coefficients compared with the standard model output (Table 3). Statistical power for the interaction between density condition and group size was $94.2 \pm 3.1\%$, indicating that small sample sizes within density conditions did not bias results. Moran's I estimates were < 0.10 with P -values > 0.05 across all distance bands, indicating no significant spatial autocorrelation in model residuals at any distance tested (Fig. S1). On average, the among-group standard deviation in random slopes for large pines was ± 0.34 (i.e. approximately 25% of the population-level coefficient estimate), suggesting that differences among individual RCW groups' home-ranges accounted for moderate changes in selection for large pines relative to the average population-level estimate for selection for large pines. The correlation between random intercepts for RCW home-range sizes and random slopes for large pines was -0.12 , indicating that selection for large pines tended to decrease slightly as RCW home-range

Table 1. Summary of Red-cockaded Woodpecker sample sizes (n), mean home-range sizes (HR; hectares), mean large pines of ≥ 35.6 cm dbh/ha (DLP), mean medium pines of 25.4–35.6 cm dbh/ha (DMP), mean hardwoods ≥ 7.6 cm dbh/ha (DHW), clutch size (Clutch) and fledgling production (Fledge) across group density conditions and group size on the Savannah River Site, South Carolina, USA, between 2014 and 2015.

Group density ^a	Group size	HR	DLP	DMP	DHW	Clutch	Fledge
Low							
$n = 5$	2	149 $\pm$ 55	14.2 $\pm$ 7.4	18.6 $\pm$ 7.1	67.0 $\pm$ 75.2	3.0 $\pm$ 1.2	1.7 $\pm$ 1.3
$n = 4$	3	214 $\pm$ 52	15.8 $\pm$ 6.2	19.8 $\pm$ 7.1	64.7 $\pm$ 68.3	3.8 $\pm$ 0.5	2.5 $\pm$ 0.6
$n = 5$	4	144 $\pm$ 52	16.9 $\pm$ 6.5	20.7 $\pm$ 7.4	61.6 $\pm$ 58.3	3.2 $\pm$ 1.3	2.4 $\pm$ 1.3
Moderate							
$n = 4$	2	139 $\pm$ 54	15.9 $\pm$ 7.5	19.8 $\pm$ 6.3	44.9 $\pm$ 59.5	3.2 $\pm$ 1.3	1.1 $\pm$ 1.2
$n = 4$	3	123 $\pm$ 54	19.4 $\pm$ 7.6	22.8 $\pm$ 8.5	48.2 $\pm$ 55.9	2.8 $\pm$ 1.5	1.1 $\pm$ 1.4
$n = 2$	4	206 $\pm$ 72	18.9 $\pm$ 7.4	24.7 $\pm$ 8.1	40.6 $\pm$ 63.4	3.0 $\pm$ 0.0	1.5 $\pm$ 0.7
High							
$n = 2$	2	95 $\pm$ 16	18.2 $\pm$ 6.3	22.8 $\pm$ 7.7	43.1 $\pm$ 66.5	3.5 $\pm$ 0.7	1.5 $\pm$ 0.7
$n = 4$	3	130 $\pm$ 28	19.4 $\pm$ 6.9	24.2 $\pm$ 8.0	42.3 $\pm$ 58.2	3.2 $\pm$ 1.0	2.5 $\pm$ 1.7
$n = 4$	4	141 $\pm$ 17	20.8 $\pm$ 7.5	24.0 $\pm$ 8.0	40.0 $\pm$ 49.2	4.5 $\pm$ 1.7	3.2 $\pm$ 1.5
Pooled							
$n = 11$	2	140 $\pm$ 54	15.3 $\pm$ 7.5	19.5 $\pm$ 6.8	53.9 $\pm$ 67.7	3.2 $\pm$ 1.2	1.5 $\pm$ 1.2
$n = 12$	3	165 $\pm$ 55	17.8 $\pm$ 7.1	21.9 $\pm$ 8.0	53.8 $\pm$ 62.9	3.0 $\pm$ 1.2	1.9 $\pm$ 1.7
$n = 11$	4	155 $\pm$ 50	18.7 $\pm$ 7.3	22.7 $\pm$ 8.0	49.5 $\pm$ 57.2	3.6 $\pm$ 1.4	2.5 $\pm$ 1.4
All							
$n = 34$	2.8 $\pm$ 0.8	151 $\pm$ 55	16.8 $\pm$ 7.5	20.9 $\pm$ 7.6	52.9 $\pm$ 64.0	3.2 $\pm$ 1.3	1.8 $\pm$ 1.4

Values reported are means $\pm$ 1 sd. ^aCalculated as number of groups per 50 ha of foraging habitat: Low = 0.42 groups/50 ha; Moderate = 0.58 groups/50 ha; High = 0.77 groups/50 ha.

Table 2. Summary of candidate resource selection models for foraging Red-cockaded Woodpecker groups ($n = 34$) on the Savannah River Site, South Carolina, USA, between 2014 and 2015. Colons denote interaction terms.

Resource selection candidate models ^{a,b}	ΔAIC_c	AIC_w
Group density: Group size:	0.0	0.92
Distance: (DLP + DMP) + DHW ^c		
Group density: Distance:	2.8	0.07
(DLP + DMP + DHW)		
Group size: Distance:	13.6	< 0.001
(DLP + DMP + DHW)		
Distance: (DLP + DMP + DHW)	38.5	< 0.001
Distance (null)	703.7	< 0.001

^aDistance = Distance to groups' cavity tree cluster (m); DLP = LiDAR-derived pines ≥ 35.6 cm dbh/ha; DMP = LiDAR-derived pines 25.4–35.6 cm dbh/ha; DHW = LiDAR-derived hardwoods ≥ 7.6 cm dbh/ha; Group size = breeding pair plus any additional helper individuals; Group density = number of Red-cockaded Woodpecker groups per 50 ha of habitat. ^bAll resource selection models were fit with DLP and Red-cockaded Woodpecker group home-range size as random slope and intercept terms, respectively. ^cWe could not fit DHW in four-way interactions due to model convergence issues.

sizes increased. However, there were no clear relationships between random intercepts and random slopes (Fig. S2).

Consistent with prediction 1, at low and moderate group density, all RCW groups selected large pines farther from the cavity tree cluster (Table 4). Consistent with predictions 2 and 3, at high group density, larger groups travelled further to select large pines, whereas smaller groups selected large pines only when they were close to the cavity tree cluster (Fig. 2). At high group density, odds ratios indicated that for every 1-unit increase in the interaction term for distance from cavity tree cluster and large pines/ha, the expected probability of use decreased by 25% for RCW groups of two birds, but increased by 47% and 88% for RCW groups of three and four or more birds, respectively (Table 4).

Consistent with prediction 4, at high group density, larger groups did not travel greater distances compared with smaller groups to select for medium pines (Fig. 3). In contrast, consistent with prediction 5, selection for medium pines increased with distance for smaller groups (Fig. 3). At high group density, odds ratios indicated that for every 1-unit increase in the interaction term for distance from cavity tree cluster and medium pines/ha, the expected probability of use increased by 119%, 99% and 74% for RCW groups of two, three and four or more birds, respectively (Table 5). Further,

Table 3. Coefficient estimates (β), 95% confidence intervals (95% CI), bootstrapped coefficient estimates (β_{boot}) and 95% bootstrapped confidence intervals (95% CI_{boot}) for the top supported third-order resource selection model for foraging Red-cockaded Woodpecker groups ($n = 34$) on the Savannah River Site, South Carolina, USA, between 2014 and 2015. Colons denote interaction terms.

Term	β	95% CI	β_{boot}	95% CI _{boot}
Intercept	-5.53***	-6.80, -4.27	-5.52***	-6.01, -5.08
Low density	1.62	-0.78, 4.03	1.64***	0.78, 2.58
Mod density	-0.75	-2.69, 1.19	-0.68	-1.42, 0.15
Group size	0.60**	0.19, 1.00	0.60***	0.45, 0.75
Distance	-0.66	-2.18, 0.87	-0.64	-1.29, -0.01
DLP	1.34*	0.14, 2.54	1.30***	0.84, 1.84
DMP	0.81	-0.45, 2.07	0.83**	0.29, 1.33
DHW	-0.70***	-0.77, -0.62	-0.69***	-0.73, -0.65
Distance: DLP	-2.00**	-3.49, -0.50	-1.99***	-2.70, -1.32
Distance: DMP	0.51	-1.11, 2.12	0.51	-0.26, 1.25
Low density: Group size	-0.25	-0.99, 0.48	-0.26	-0.52, 0.00
Mod density: Group size	0.15	-0.52, 0.82	0.12	-0.16, 0.38
Low density: Distance	-1.63	-4.62, 1.37	-1.58*	-2.91, -0.26
Mod density: Distance	1.16	-1.05, 3.37	1.12*	0.13, 2.04
Low density: DLP	4.79***	2.45, 7.14	4.87***	3.90, 5.77
Mod density: DLP	2.59**	0.81, 4.38	2.57***	1.81, 3.35
Low density: DMP	-5.82***	-8.19, -3.46	-5.92***	-6.74, -5.05
Mod density: DMP	-1.59	-3.56, 0.38	-1.66***	-2.47, -0.67
Low density: Distance: DLP	-6.58***	-9.58, -3.58	-6.70***	-8.24, -5.16
Mod density: Distance: DLP	-3.49**	-5.60, -1.38	-3.49***	-4.52, -2.51
Low density: Distance: DMP	7.16***	4.01, 10.32	7.27***	5.84, 8.54
Mod density: Distance: DMP	2.05	-0.35, 4.45	2.12***	0.68, 3.23
Group size: Distance	-0.44	-0.91, 0.03	-0.45***	-0.64, -0.29
Group size: DLP	-0.20	-0.59, 0.19	-0.18*	-0.34, -0.02
Group size: DMP	-0.41*	-0.82, 0.00	-0.43***	-0.59, -0.24
Group size: Distance: DLP	0.46*	0.00, 0.92	0.45***	0.25, 0.68
Group size: Distance: DMP	-0.06	-0.56, 0.45	-0.04	-0.28, 0.19
Low density: Group size: Distance	0.21	-0.68, 1.10	0.20	-0.18, 0.57
Mod density: Group size: Distance	-0.42	-1.15, 0.30	-0.40*	-0.71, -0.05
Low density: Group size: DLP	-1.26***	-1.97, -0.54	-1.28***	-1.57, -0.99
Mod density: Group size: DLP	-1.03**	-1.66, -0.39	-1.01***	-1.31, -0.73
Low density: Group size: DMP	1.39***	0.66, 2.12	1.41***	1.15, 1.70
Mod density: Group size: DMP	0.79*	0.11, 1.48	0.81***	0.45, 1.12
Low density: Group size: Distance: DLP	1.74***	0.86, 2.62	1.76***	1.32, 2.15
Mod density: Group size: Distance: DLP	1.29***	0.59, 1.98	1.28***	0.91, 1.60
Low density: Group size: Distance: DMP	-1.76***	-2.70, -0.82	-1.78***	-2.13, -1.36
Mod density: Group size: Distance: DMP	-0.79*	-1.58, 0.00	-0.81***	-1.17, -0.31

Distance = Euclidian Distance to groups' cavity tree cluster; DLP = LiDAR-derived pines ≥ 35.6 cm dbh/ha; DMP = LiDAR-derived pines 25.4–35.6 cm dbh/ha; DHW = LiDAR-derived hardwoods ≥ 7.6 cm dbh/ha; Group size = breeding pair plus any additional helper individuals; Low/Moderate density = factors for number of Red-cockaded Woodpecker groups per 50 ha of habitat (Low density = 0.42 groups/50 ha; Moderate density = 0.58 groups/50 ha; High density (Reference condition) = 0.77 groups/50 ha). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

at high group density, groups of two to three birds selected medium pines farther from the cavity tree cluster, whereas groups of four or more birds neither selected nor avoided medium pines at any distance from the cavity tree cluster (Fig. 3). At low group density, all group sizes were likely to select medium pines as distance from the cavity tree cluster increased, although at moderate group density, larger groups were more likely to travel

farther to select medium pines compared with smaller groups (Table 5, Fig. 3).

DISCUSSION

Results from this study provide preliminary evidence that trade-offs between foraging and territorial defence in group-territorial species are shaped by the competitive advantage of larger groups at

Table 4. Odds ratios (± 1 se), 95% confidence intervals (95% CI) and Tukey groupings (Tukey), for effects of distance to cavity tree cluster on selection for large pines (≥ 35.6 cm dbh/ha) (Distance $\times$ DLP), by foraging Red-cockaded Woodpecker groups ($n = 34$) of different sizes (Group size) across group density conditions on the Savannah River Site, South Carolina, USA, between 2014 and 2015.

Group density	Group size	Distance $\times$ DLP	95% CI	Tukey
Low	2	1.87 ± 0.04	1.79, 1.96	A
	3	1.83 ± 0.03	1.77, 1.90	A
	4	1.79 ± 0.06	1.68, 1.91	A
Moderate	2	1.69 ± 0.04	1.61, 1.78	A
	3	1.58 ± 0.05	1.47, 1.69	A
	4	1.45 ± 0.12	1.21, 1.69	A
High	2	0.75 ± 0.22	0.32, 1.18	A
	3	1.47 ± 0.11	1.26, 1.67	B
	≥ 4	1.88 ± 0.08	1.73, 2.03	C

Distance = Euclidian Distance to groups' cavity tree cluster; DLP = LiDAR-derived pines ≥ 35.6 cm dbh/ha; Group size = breeding pair plus any additional helper individuals; Low/Moderate density = factors for number of Red-cockaded Woodpecker groups per 50 ha of habitat (Low density = 0.42 groups/50 ha; Moderate density = 0.58 groups/50 ha; High density (Reference condition) = 0.77 groups/50 ha).

high group density. Larger group sizes are likely to allow RCWs to monopolize distant large pines with a low risk of being displaced by smaller groups encountered at the distant resource. The competitive advantage of larger RCW groups at high group density entails substantial costs to smaller groups and essentially reverses the effect of

distance on selection for large pines observed for smaller groups at low group density. The reversal of distance effects on selection for large pines at high group density indicates that costs of among-group competition tend to partition high-quality distant foraging resources in favour of larger groups. This is likely to be due to within-group cooperation that spreads costs of travel and competition across several group members (Arnold *et al.* 2005). This numerical advantage could explain how larger RCW groups are able to displace smaller groups from large pines in overlapping foraging areas at high group density. White-breasted Thrashers *Ramphocinclus brachyurus* that live in cooperative groups, for instance, have greater capacity to switch between incubation and foraging without reducing fitness compared with lone pairs because helpers assist with territorial defence while breeding males provision nests (Mortensen & Reed 2018). Similarly, increases in RCW group size improve foraging efficiency because helpers share the costs of territorial defence (Conner *et al.* 1999) and selecting distant high-quality resources (Canestrari *et al.* 2008a,b).

Given the tendency of large groups to monopolize distant high-value foraging resources, traditional Thiessen foraging partitions should be used with caution when RCW group density is high. Thiessen foraging partitions are used to equally allocate foraging habitat among neighbouring RCW groups based solely on distances between cavity tree clusters, and offer managers a rapid and

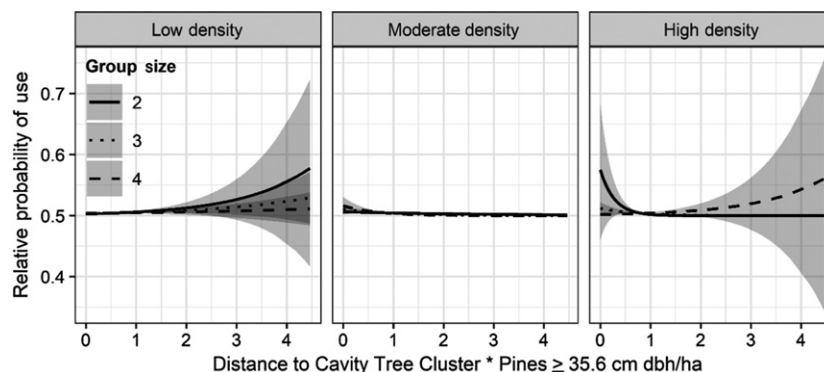


Figure 2. Predicted relative probability of use by foraging Red-cockaded Woodpecker group sizes of 2, 3 and 4, at low, moderate and high group density across the range of observed values for the interaction between scaled distance from cavity tree clusters (m) and LiDAR-derived large pines (≥ 35.6 cm dbh/ha) (Distance to Cavity Tree Cluster $\times$ DLP). Black lines and shaded regions represent predicted relative probability of use and 95% confidence intervals. Predictions are based on data for 14 groups at low group density ($n = 5$, $n = 4$ and $n = 5$ for group sizes 2, 3 and 4, respectively), for 10 groups at moderate group density ($n = 4$, $n = 4$ and $n = 2$ for group sizes 2, 3 and 4, respectively), and for 10 groups at high group density ($n = 2$, $n = 4$ and $n = 4$ for group sizes 2, 3 and 4, respectively).

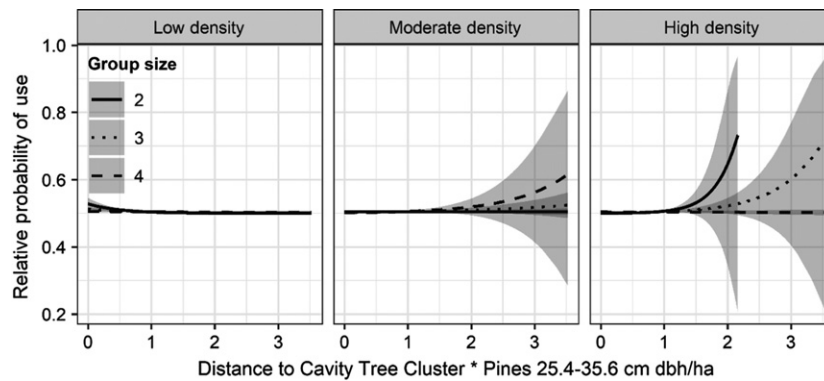


Figure 3. Predicted relative probability of use by foraging Red-cockaded Woodpecker group sizes of 2, 3 and 4, at low, moderate and high group density across the range of observed values for the interaction between scaled distance from cavity tree clusters (m) and LiDAR-derived pines 25.4–35.6 cm dbh/ha (Distance to Cavity Tree Cluster $\times$ Pines 25.4–35.6 cm dbh/ha). Black lines and shaded regions represent predicted relative probability of use and 95% confidence intervals. Predictions are based on data for 14 groups at low group density ($n = 5$, $n = 4$ and $n = 5$ for group sizes 2, 3 and 4, respectively), for 10 groups at moderate group density ($n = 4$, $n = 4$ and $n = 2$ for group sizes 2, 3 and 4, respectively) and for 10 groups at high group density ($n = 2$, $n = 4$ and $n = 4$ for group sizes 2, 3 and 4, respectively).

Table 5. Odds ratios (± 1 se), 95% confidence intervals (95% CI) and Tukey groupings (Tukey), for effects of distance to cavity tree cluster on selection for medium pines (25.4–35.6 cm dbh/ha) (Distance $\times$ DMP), by foraging Red-cockaded Woodpecker groups ($n = 34$) of different sizes (Group size) across group density conditions on the Savannah River Site, South Carolina, USA, between 2014 and 2015.

Group density	Group size	Distance $\times$ DMP	95% CI	Tukey
Low	2	1.75 ± 0.06	1.64, 1.87	A
	3	1.85 ± 0.05	1.76, 1.94	A
	4	1.94 ± 0.08	1.78, 2.10	A
Moderate	2	1.33 ± 0.09	1.14, 1.52	A
	3	1.54 ± 0.05	1.44, 1.63	AB
	4	1.71 ± 0.07	1.56, 1.85	B
High	2	2.19 ± 0.10	1.99, 2.39	A
	3	1.99 ± 0.06	1.87, 2.11	AB
	≥ 4	1.74 ± 0.10	1.55, 1.93	B

Distance = Euclidian Distance to groups' cavity tree cluster; DMP = LiDAR-derived pines 25.4–35.6 cm dbh/ha; Group size = breeding pair plus any additional helper individuals; Low/Moderate density = factors for number of Red-cockaded Woodpecker groups per 50 ha of habitat (Low density = 0.42 groups/50 ha; Moderate density = 0.58 groups/50 ha; High density (Reference condition) = 0.77 groups/50 ha).

standardized approach to delineate critical foraging habitat at the landscape scale without the need for detailed home-range data. Previous studies have highlighted poor performance of Thiessen partitions at high group density because they do not capture increases in home-range overlap (Garabedian *et al.* 2018a). Our study shows that differences in group

size at high group density further complicate use of Thiessen foraging partitions by influencing accessibility of distant large pines for small groups. Based on our results, even if a small group's Thiessen foraging partition includes many large pines, if the large pines are not close to the cavity tree cluster, they may not be accessible in the presence of larger neighbouring groups. Therefore, in areas where group density is high, for example because of budding or installation of new recruitment clusters (i.e. installation of artificial cavities in unoccupied RCW habitat; Copeyon *et al.* 1991, USFWS 2003), smaller groups are likely to have low reproductive success over the short term because costs from foraging competition are substantial for small groups at high group density. These relationships suggest that conservation efforts for group-territorial, central-place foraging birds should prioritize establishment of larger group sizes where group density is high to mitigate negative effects of foraging competition on reproductive success.

Selection for large pines only when close to the cavity tree cluster at high group density is important to the long-term fitness of small RCW groups because it allows them to maximize benefits from both territorial defence and selecting high-quality resources. By trading off selection for distant large pines with territorial defence, breeders in small groups are more likely to maintain their breeding position and territory occupancy, which provide long-term fitness benefits that may outweigh the current year's reproductive success (Ydenberg &

Krebs 1987). Smaller groups stand to gain more from the trade-off between selection of distant large pines with territorial defence than are larger groups because competition for breeding positions is intense and cavity trees are considered the most limiting resource for RCW populations (Walters 1991). Differences in selection that reduce competition costs may also be a strategy to conserve resources for future reproduction, which may be particularly important for breeding females in small groups (Browning *et al.* 2012). Selection for uncontested medium pines further from the cavity tree cluster could allow smaller groups passively to gain social information about neighbouring groups that indirectly improves demographic connectivity and group persistence (Garabedian *et al.* 2018b). Because the costs of competition at high group density are exacerbated for small groups, selection for large pines only when they are close to the cavity tree cluster is likely to reflect a 'home-field' advantage that offsets the competitive abilities of larger groups (Zack & Rabenold 1989, Strong *et al.* 2018). The relative distance to the central place is a primary factor determining the winner of territorial contests in other species of group-territorial central-place foraging birds (Brown 1982, Ydenberg & Houston 1986). Thus, at high group density it becomes more beneficial for smaller foraging RCW groups to select large pines close to the cavity tree cluster or, alternatively, distant medium pines that are uncontested by larger neighbouring groups.

Our results suggest that lower reproductive success typically observed in smaller groups is due to changes in foraging behaviours at high group density rather than differences in arthropod prey availability between medium and large pines. Because arthropod prey delivered to nestlings are similar in poor- and high-quality habitat (Hanula & Engstrom 2000, Hanula *et al.* 2000b), and provisioning rates do not differ between low and moderate group density conditions (Conner *et al.* 1999), it may be that smaller groups need relatively more time to acquire large arthropod prey from medium pines than large pines. Delivery of larger loads from distant medium pines may be possible for small RCW groups because they can forage without competition from larger groups (Ydenberg *et al.* 1986). It is possible that the reduced competition allows smaller RCW groups to increase foraging effort and provisioning rates when selecting distant medium pines, thereby gaining fitness benefits comparable to those gained

from selecting large pines at the same distance. White-backed Woodpeckers *Dendrocopos leucotos*, for example, maintain high productivity by adjusting foraging behaviours when selecting different substrates (Lorenz *et al.* 2016). Alternatively, at high group density, adults in smaller RCW groups may select distant medium pines primarily for self-provision because they can readily consume smaller arthropod prey that would not offset costs of provisioning nests from distant resources. Hence, smaller RCW groups at high group density may forage on large pines close to the cavity tree cluster where they can more frequently provision nests with large arthropods, but otherwise will select distant medium pines when foraging for themselves. Selection for medium pines at high group density also may facilitate use of social information that provides long-term indirect benefits compensating for reduced foraging efficiency at high group density, as observed in other bird species (Fletcher 2007, Andrews *et al.* 2015).

Our study contributes to the understanding of density-dependent resource selection by identifying differences in the way that large and small groups of territorial central-place foragers manage trade-offs in resource selection to optimize fitness at high group density. Foraging interference is a main determinant of the travel costs incurred by group-territorial central-place foraging birds (Brown 1982) and our study highlights that there can be substantive differences in the costs and benefits of selecting resources due to differences in RCW group size and group density. The cost of competing with larger RCW groups at high group density alters foraging behaviours of smaller groups and leads to the trade-off between selecting distant high-quality large pines and territorial defence. Ensuring that a sufficient number of large pines are within RCW territories will reduce the likelihood that smaller groups will compete for access to distant large pines and the costs of territorial defence at high group density until group sizes increase over time. Many group-territorial animals adjust foraging behaviours to reduce costs of intraspecific competition that limit access to high-quality resources (Matthiopoulos 2003, McLoughlin *et al.* 2006, Rozen-Rechels *et al.* 2015). Accounting for group size and group density effects in studies of resource selection can reveal how groups of different sizes optimize fitness at high group density through trade-offs between territorial defence and selecting distant high-quality resources.

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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 I estimates assessing spatial autocorrelation in resource selection model residuals at 23 distance bands between 1 and 5000 m.

Figure S2. Scatterplot of random term estimates (Estimate; *x*-axis) illustrating relationships between estimates of baseline selection (Random Intercept) and selection for pines ≥ 35.6 cm dbh/ha (Random Slope) conditional on Red-cockaded Woodpecker home-range sizes ($n = 34$; *y*-axis) on the Savannah River Site, South Carolina, USA, between 2014 and 2015.

Table S1. Red-cockaded Woodpecker home-range behaviours observed for groups in low, moderate and high group density conditions on the Savannah River Site, South Carolina, USA, between 2014 and 2015.