# Evaluating interactions between space-use sharing and defence under increasing density conditions for the group-territorial Red-cockaded Woodpecker *Leuconotopicus borealis*

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Information about how bird species respond to increasing density conditions through either space-use sharing or increased territoriality, and how those changes affect fitness, is essential for effective conservation planning. We used a case study of endangered Red-cockaded Woodpeckers *Leuconotopicus borealis* (RCW) to address these questions. We documented over 36 000 locations from 44 RCW groups in three density conditions on two sites in South Carolina, USA, between April 2013 and March 2015. The frequency of neighbouring group interactions differed among density conditions and was highest for high-density groups. RCW home-ranges and core-areas were larger under low-density conditions ($\bar{x}_{\text{Home-range}} = 88.4$ ha, $\bar{x}_{\text{Core-area}} = 21.0$ ha) than under medium ($\bar{x}_{\text{Home-range}} = 68.29$ ha, $\bar{x}_{\text{Core-area}} = 16.6$ ha) and high-density ($\bar{x}_{\text{Home-range}} = 76.3$ ha, $\bar{x}_{\text{Core-area}} = 18.6$ ha) conditions. Neighbouring RCWs maintained overlapping home-ranges with nearly exclusive core-areas across density conditions, but overlap tended to increase as neighbouring group density increased. Under high-density conditions, home-range overlap correlated inversely with clutch size ($\beta \pm \text{se} = -0.19 \pm 0.09$), nestling production ($\beta \pm \text{se} = -0.37 \pm 0.09$) and fledgling production ($\beta \pm \text{se} = -0.34 \pm 0.08$). Our results indicate that RCWs dedicate more effort to territorial defence under high-density conditions, potentially at the expense of greater foraging efficiency and time allocated to reproduction, as evidenced by reduced fitness. Large home-range overlap indicated limited territoriality farther away from cavity trees, but the existence of exclusive core-areas suggests that RCW groups defend habitat closer to cavity trees. Thiessen partitions used to allocate critical foraging habitat offered comprehensive habitat protection for RCW but appear flawed for spatially explicit habitat assessments because they do not accurately delineate space used by individual RCW groups.

**Keywords:** core-area, density dependence, fitness, home-range, overlap, Red-cockaded Woodpecker, resident species, territoriality, Thiessen polygons.

Knowledge of home-range and territory characteristics offers practical guidance for conservation of territorial resident birds with limited habitat (Adams 2001). Estimates of home-range size are valuable for conservation efforts such as reserve design (Villarreal *et al.* 2014, Hartmann *et al.* 2017) and determining minimum area requirements for recovery of endangered species (Hernández *et al.* 2006, Smith *et al.* 2016). Home-range shapes can be used to guide local management strategies, such as identifying locations for food supplementation (López-López *et al.* 2014), selecting sites for habitat restoration (Bennett *et al.* 2012, 2013, Stanton *et al.* 2015) and determining

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compliance with regulatory guidelines for recovery of endangered species (Fedy *et al.* 2014, Garabedian *et al.* 2014b). Home-range overlap and effects on fitness can be important to identify spacing requirements that minimize competition and optimize species productivity (Mänd *et al.* 2009, Kašová *et al.* 2014, Sharps *et al.* 2015).

Home-ranges, like territories, are plastic in the sense that birds routinely adapt them in response to individual condition (e.g. age, reproductive status), available food resources, nest-sites or conspecific density (Andrewartha & Birch 1954, Schoener 1968, Ford 1983, Smith & Shugart 1987). A large home-range or territory that includes abundant food may lead to higher fitness, but abundant food also may attract conspecifics to the area and increase competition (Brown 1969, Hixon 1980). Birds may respond to increases in conspecific density and competition by reducing the size of home-ranges and territories, but is there likely to be a minimum size required to supply the resources needed for survival and reproduction (Nice 1941, Enoksson & Nilsson 1983, Both *et al.* 2000)? Alternatively, birds may respond to increases in conspecific density by defending only the intensively used area around the nest-site (Brown & Orians 1970, Both & Visser 2003). Defence of smaller, intensively used areas within larger home-ranges that overlap with neighbouring conspecifics may be common in territorial birds (Potts *et al.* 2014). Even during the breeding season, home-ranges of territorial birds can extend beyond the defended territory (Anich *et al.* 2009, Streby *et al.* 2012).

Home-range overlap has been associated with increases in conspecific density in many species, but how resident territorial birds partition use of overlapping areas is not well understood (Stamps 1990, López-Sepulcre & Kokko 2005). Avoidance of overlapping areas could be a mechanism to reduce the frequency of agonistic interactions (Moorcroft *et al.* 2006). Some territorial birds tolerate overlap with conspecifics in areas with abundant resources, but avoid defended areas surrounding neighbouring nest-sites (Goldenberg *et al.* 2016). Other birds maintain high home-range overlap but avoid direct interaction with neighbouring conspecifics through temporal partitioning (Anich *et al.* 2009). Increases in home-range overlap can have a direct effect on the fitness of territorial resident birds, but only limited research has explored these relationships (Newton 1992, Both 1998, López-Sepulcre *et al.* 2009).

Behavioural observations can provide further insight into the interplay between space-use overlap and fitness in resident birds that maintain all-purpose territories throughout the year (Krüger *et al.* 2012, Grünkorn *et al.* 2014, Schuppe *et al.* 2016). Home-range overlap suggests that resources or space are partitioned to some degree, which can increase the frequency of competitive interactions (Ims 1987, Stamps 1990). Crowding effects and increased intraspecific competition under high population densities could require birds to dedicate more time to territorial defence at the expense of nestling provisioning (Sillett *et al.* 2004, Bretagnolle *et al.* 2008). Reduced foraging rates at greater levels of competition lead to greater mortality in adults (Stillman *et al.* 2000) and nestlings (Fielding 2004). Additionally, competitive interactions can influence the configuration of home-ranges or territories, which in turn may influence accessibility of limited resources (Krebs 1971, Adams 2001, Kokko & Lundberg 2001). For example, territorial interactions between neighbouring conspecifics may exacerbate seasonal food limitations (Fernández-Bellon *et al.* 2016) or access to limited nest-sites (Pasinelli *et al.* 2001) by preventing expansion of home-range or territory boundaries.

Research on variation in space-use characteristics and behaviours in response to variation in conspecific density would benefit conservation of the endangered Red-cockaded Woodpecker *Leuconotopicus borealis* (RCW). The RCW is a group-territorial, resident bird endemic to pine *Pinus* spp. forests of the southern USA (U.S. Fish and Wildlife Service (USFWS) 1970, 2003). Habitat loss, particularly of Longleaf Pine *Pinus palustris* forests and old pines required for nesting and roosting, was the primary historical cause of the species' decline (Ligon *et al.* 1986, Conner *et al.* 2001). As nesting constraints are now mitigated through techniques such as prescribed burning and artificial cavity construction (Copeyon 1990, Allen 1991), foraging habitat management has gained importance in RCW recovery (Walters *et al.* 2002). The most appropriate method to delineate foraging habitat to individual RCW groups is using home-range data. However, this approach is resource-intensive and rarely used (Convery & Walters 2004). Alternatively, the USFWS recommends use of Thiessen polygons to create non-overlapping foraging partitions that delineate an 800-m radius around each cluster of trees with nest cavities such

that the partition boundaries divide space equally among all neighbouring RCW groups (hereafter, Thiessen partitions; Lipscomb & Williams 1995). Although standard Thiessen partitions provide a reasonable method to delineate RCW foraging habitat, considerable variation in RCW home-range sizes raises uncertainty about whether this method accurately represents home-range or territory characteristics under variable density conditions (Garabedian *et al.* 2014b).

RCWs are an ideal focal species for determining how resident territorial species adjust behaviours to balance space-use sharing and defence as population density changes, and how these adjustments may influence group reproductive success. RCW groups defend territories that include cavity trees and adjacent foraging habitat, and their home-ranges may extend well beyond the defended territory (Hooper *et al.* 1982, James *et al.* 1997, 2001). RCWs are known to exhibit strong territoriality to exclude conspecifics from the proximity of the cavity tree cluster (Ligon *et al.* 1986, Lennartz *et al.* 1987) but the degree to which territorial defence extends to the entire area delineated by Thiessen partitions is uncertain. Because the application of Thiessen partitions for habitat delineation assumes that neighbouring RCWs partition space into discrete territories with no overlap (Nilsen *et al.* 2007, Schlicht *et al.* 2014), reports of overlapping home-ranges (Engstrom & Sanders 1997) suggest the method could be flawed when applied to high-density populations. We investigated RCW home-range dynamics across a gradient of neighbouring group density conditions. Specifically, our objectives were: (1) to investigate space-use sharing and territoriality by neighbouring RCW groups across a gradient of local neighbouring group density conditions; (2) to determine whether home-range dynamics change with neighbouring group density and if those changes influence RCW group fitness; and (3) to evaluate concordance between USFWS foraging partitions and RCW space-use estimates in the context of space-use sharing and territorial behaviours. We predicted that increased conspecific density would lead to greater home-range overlap and frequency of territorial interactions among neighbouring RCW groups and that increased home-range overlap would reduce RCW reproductive success, particularly for neighbouring groups under high-density conditions. Additionally, we predicted that the most intensively used areas around group cavity tree clusters would be defended as territories and are thus distinguished from the larger home-range that overlaps with neighbouring RCW groups.

## METHODS

### Study areas

The Savannah River Site (33°15′N, 81°38′W), 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 physiographical provinces in South Carolina, USA. The Savannah River 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, most of the Savannah River Site was maintained as agricultural fields; recently, it has been harvested for timber (White 2005). The U.S. Department of Agriculture Forest Service has managed the natural resources of the Savannah River Site since 1952 and reforested most of it (Imm & McLeod 2005, White 2005). Approximately 53 014 ha of the Savannah River Site is now reforested with artificially regenerated stands of Loblolly *Pinus taeda*, Longleaf Pine and Slash Pine *Pinus elliottii* with an additional 2832 ha of pine–hardwood mixtures (Imm & McLeod 2005). The remaining 27 000 ha of forested area on the Savannah River Site consists of bottomland hardwoods, forested swamps/ streams and mixed-hardwood stands. Under intensive management since 1985, the RCW population has grown from three groups of four birds (Johnston 2005) to 91 active groups of more than 250 birds in 2016 (T. Mims, pers. comm.).

The Carolina Sandhills National Wildlife Refuge (34°35′N, 80°14′W), one of 14 Land Management and Research Demonstration areas managed by the USFWS, is located on the Atlantic Coastal Plain and Piedmont Plateau physiographical provinces, South Carolina, USA. The Carolina Sandhills National Wildlife Refuge is characterized by sandy soils dominated by upland, xeric pine woodlands. The refuge was established in 1939 from federal efforts to acquire eroded and abused lands from landowners who were provided with alternative, more productive lands elsewhere (USFWS 2010). The refuge is approximately 19 364 ha, including 14 164 ha of predominantly Longleaf Pine and Turkey Oak *Quercus cerris* cover (USFWS 2010). The refuge harbours 150 active
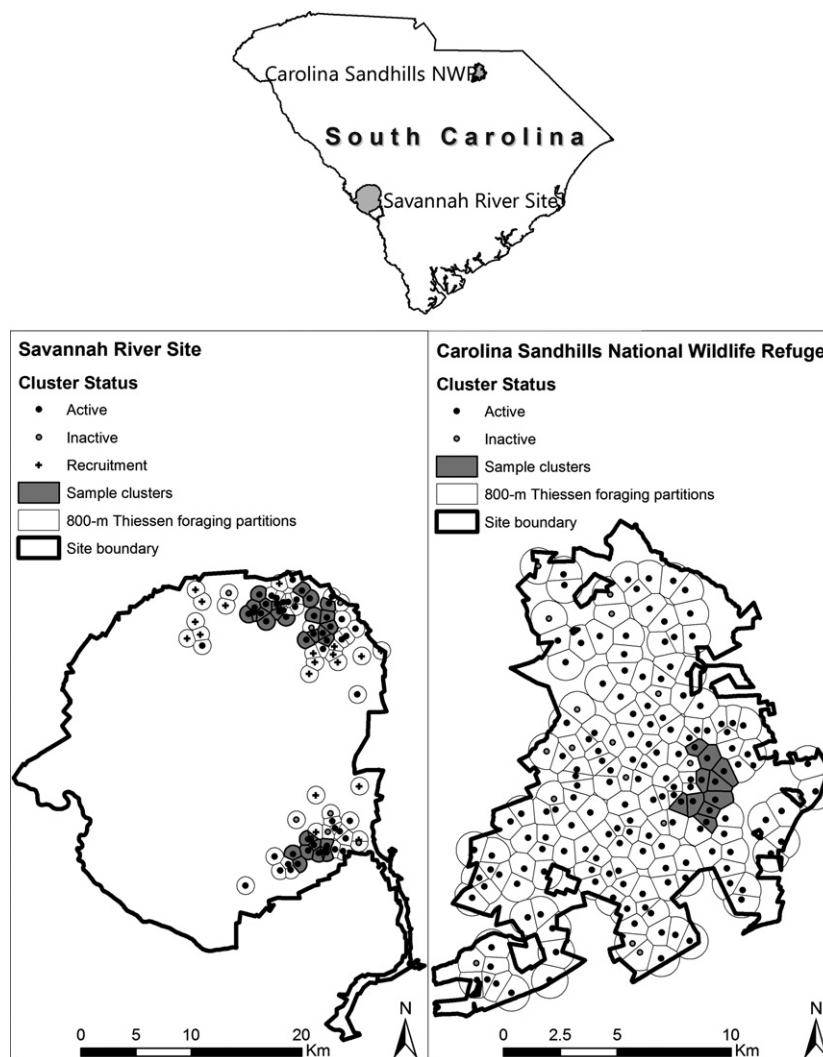
**Figure 1.** The spatial distribution and status of Red-cockaded Woodpecker cavity tree clusters on Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, USA, in 2013.

RCW clusters, representing the largest RCW population on USFWS lands.

## Data collection

### RCW sample selection

We collected home-range data for 44 RCW groups between April 2013 and March 2015 (Fig. 1). Individual RCW nest-site clusters were considered for sample selection if they had been active with a potential breeding group (a breeding male and breeding female occupying the same cavity tree cluster) minimally for the past 2 years and had not been identified as a 'captured cluster' (a secondary cluster within the home-range of an RCW group) since 2011. We selected these criteria to increase the likelihood that clusters remained active with a potential breeding group throughout the study. We mapped the distribution of RCW clusters that satisfied these two primary selection criteria using GIS to examine visually the spatial configuration of potential sample clusters (ESRI 2014). Using the map of potential sample clusters, we created 10-cluster aggregates for which the only selection criterion was that individual clusters within an aggregate were not separated by > 1 Thiessen foraging partition.

We calculated neighbouring group density as the number of groups per 50 ha of foraging

habitat delineated by 800-m Thiessen partitions for RCWs within 10-cluster aggregates; we selected 50 ha to approximate the recommended minimum amount of good-quality foraging habitat allocated to individual clusters (49 ha; USFWS 2003). Based on previous research, we considered ranges of 0.10–0.50, 0.51–1.00 and > 1.00 groups/50 ha to represent low, medium and high neighbouring group density conditions, respectively. Researchers have suggested that one RCW group per 50 ha represents a 'high' density population (Hooper & Lennartz 1995), one group per 128 ha (or 0.39 groups/50 ha) represents a 'moderate' density population (Conner *et al*. 1999) and one group per 212 ha (0.23 groups/50 ha) represents a 'low' density population (Conner *et al*. 1999). Neighbouring group density estimates for low, medium and high-density conditions in 2013 were approximately 0.42 groups/50 ha (Savannah River Site), 0.60 groups/50 ha (Savannah River Site) and 0.85 groups/50 ha (Carolina Sandhills National Wildlife Refuge), respectively. Neighbouring group density estimates for low, medium and high-density conditions in 2014 were approximately 0.39 groups/50 ha (Savannah River Site), 0.57 groups/50 ha (Savannah River Site) and 0.85 groups/50 ha (Carolina Sandhills National Wildlife Refuge), respectively. In 2014, we sampled an additional 10 groups under high-density conditions on the Savannah River Site; the estimated neighbouring group density for this sample was approximately 0.77 groups/50 ha.

### RCW fitness data

As part of ongoing monitoring, agency personnel on each site conducted RCW group observations and nest checks to determine clutch size, nestling production, fledgling production and group size for each RCW cluster. We characterized these parameters for the 44 sample groups using the annual means from 2009 to 2013 for each group. We included group size because larger RCW groups tend to have greater reproductive success (Walters 1990, Khan & Walters 2002). Clutch size, nestling production and fledgling production data were averaged using observations from 2009 to 2013. Group size data collected on the Savannah River Site were averaged using observations from 2010 to 2013 because group size data from 2009 were unavailable.

### Home-range surveys

We followed foraging RCW groups for a minimum of 4 h on any given day, recording location fixes at 15-min intervals (Franzreb 2006), twice a month between March 2013 and April 2015. Minimally, we recorded 15 location fixes throughout the day during each observation period, thus providing ≥ 30 relocations per month. In addition to location fixes, we documented basic behaviours (e.g. foraging, resting, cavity work, feeding nestlings and intra- or interspecific interactions) at each 15-min interval. Survey efforts within each month were divided into two sampling periods during which we followed each sample RCW group once; we randomized sampling order within each period. During observation periods, we maintained visual contact with individuals of the sample group beginning when individuals left their roosts in the morning and continuing until contact with the birds was lost or until terminated due to inclement weather or management activities that precluded site access (e.g. prescribed burning). We considered observation periods to be incomplete if < 15 location fixes were recorded throughout a single day and repeated data collection at a later date in the same month.

RCW group members tend to forage close to one another, even in the same tree (Franzreb 2006), so we used location fixes for the breeding male of each sample group to represent movement of the entire group. We adopted this approach for tracking RCW groups because breeding males are the most stable individuals of the group, maintaining their breeding status until they die, and breeding males tend to be the dominant individual within the social hierarchy of each group (Conner *et al*. 2001). All RCWs tracked at the Savannah River Site and Carolina Sandhills National Wildlife Refuge were uniquely colour-ringed as part of ongoing monitoring by agency personnel. We used spotting scopes to re-sight and confirm unique colour-ring combinations to ensure the breeding male was followed throughout the day.

## Space-use analysis

We used kernel density methods to estimate utilization distributions (UDs; Worton 1989) for each RCW sample group. Utilization distributions define space use as a continuous and probabilistic process throughout a predefined area and can be visualized as a three-dimensional surface reflecting the probability of use at specific locations within that area (Millspaugh *et al*. 2006). We defined the home-range and core-areas as the 95% and 50%

UD isopleths, respectively (White & Garrott 1990). We estimated annual and seasonal sizes and spatial overlap of home-ranges and core-areas for sample RCW groups in each of low, medium and high neighbouring group density conditions. We used 3-month periods to define seasons representing breeding (April to June), fledging (July to September), post-fledging (October to December) and winter (January to March). We quantified spatial overlap using the volume of intersection or the cumulative sum of the minimum volume of intersection between corresponding pixels of overlapping areas of UDs (Fieberg & Kochanny 2005). Analysis of RCW relocations and estimation of UDs was conducted in the R statistical environment (R Development Core Team 2015) using the contributed packages 'sp' (Pebesma & Bivand 2005, Bivand *et al.* 2013) and 'adehabitatHR' (Calenge 2006).

We used a chi-square test of proportions to characterize RCW home-range behaviours in two ways. First, we determined whether 800-m Thiessen foraging partitions accurately reflected RCW habitat use by comparing the proportion of RCW locations within 800-m Thiessen partitions to the proportion outside partitions. Secondly, we investigated changes in territorial behaviours by comparing the frequency of neighbouring group interactions among density conditions.

We used a mixed-effects ANOVA to compare home-range and core-area size and overlap estimates among low, medium and high neighbouring group density conditions. Fixed-effects included site, year, group size, density condition, season, and the interaction between density condition and season; individual group ID was fitted as a random effect. We used mixed-effects multiple linear regression to model relationships between RCW reproductive success and both home-range and core-area characteristics. We fitted models using mean clutch sizes, nestling production and fledgling production between 2009 and 2013 as the response variable. In each model, we fitted density as a three-level fixed effect, and group size, UD size and UD spatial overlap as covariates. We also fitted the interactions between density and UD size, and between density and UD spatial overlap. Group ID was fitted as a random effect. We removed non-significant interaction terms from home-range and core-area size, and overlapped models to improve model interpretation, but otherwise did not conduct formal model selection. Mixed-effects models were fitted in the R statistical environment (R Development Core Team 2015) using the contributed package 'lme4' (Bates *et al.* 2015).

## RESULTS

We documented over 36 000 RCW locations between April 2013 and March 2015 (Supporting Information Table S1). The average duration of completed home-range observation sessions was 5.5 h (range: 4–8 h). Approximately 98% of foraging locations were within the total area of 800-m Thiessen partitions for 10-group clusters but home-range boundaries derived from these locations often overlapped with standard Thiessen partitions of neighbouring groups (Supporting Information Figs S1–S3). Foraging and interspecific interactions were the most frequent and infrequent observations of RCWs, respectively, across all densities (Table S1). Frequency of neighbouring group interactions differed among densities and was greatest at high density ($\chi^2 = 179.26$, $df = 27$, $P < 0.001$).

### Space use and density

Across all three density conditions, home-range and core-area sizes ranged from approximately 40 to 100 and 10 to 30 ha, respectively (Fig. 2). There was no significant site effect on home-range or core-area sizes (home-range model: $F = 2.9$, $P = 0.09$; core-area model: $F = 2.5$, $P = 0.11$; Table 1). Home-ranges but not core-areas, were smaller during the second year of the study (home-range model: $F = 3.3$, $P = 0.07$; core-area model: $F = 1.0$, $P = 0.31$; Table 1). Large groups had larger home-ranges but not larger core-areas (Table 1). Home-range and core-area sizes varied among density conditions (home-range model: $F = 5.6$, $P = 0.004$; core-area model: $F = 3.5$, $P = 0.02$) and seasons (home-range model: $F = 10.2$, $P \leq 0.001$; core-area model: $F = 14.6$, $P \leq 0.001$). The interaction between density condition and season did not have a significant effect on home-range or core-area sizes (home-range model: $F = 1.2$, $P = 0.31$; core-area model: $F = 1.1$, $P = 0.43$), so we removed the interaction term to simplify model interpretation. Average RCW home-ranges and core-areas were larger at low densities than at medium or high densities (Table 1). Across
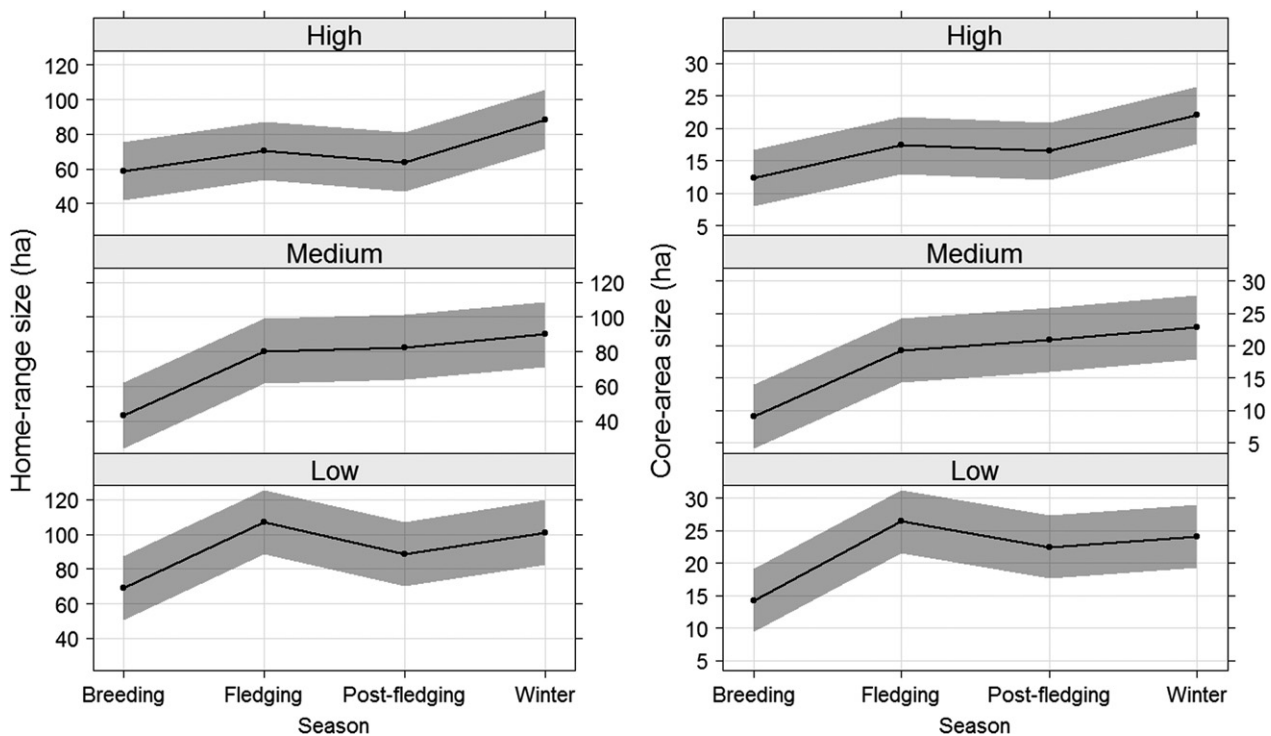
**Figure 2.** Relationships between Red-cockaded Woodpecker home-range and core-area sizes and season at low, medium and high group densities. Black circles connected by trend lines represent mean size estimates and grey bands represent 95% confidence intervals.

home-range and core-area models, sizes were smallest during the breeding season and increased during the fledging season, post-fledging season and winter season (Fig. 2).

Foraging RCW groups shared adjacent foraging habitat across all density conditions (Figs S1–S3). Spatial overlap between neighbouring groups was greater on the Carolina Sandhills National Wildlife Refuge than on the Savannah River Site (home-range model: $F = 19.3$, $P \leq 0.001$; core-area model: $F = 29.5$, $P \leq 0.001$; Table 2). Core-area overlap was slightly greater during the second year of the study (Table 2). There was no group size effect on home-range or core-area overlap (Table 2). Across home-range and core-area models, overlap estimates tended to be smallest during the breeding season and increased during the fledging, post-fledging and winter seasons (Fig. 3). The interaction between density condition and season had a significant effect on home-range and core-area overlap (home-range model: $F = 3.3$, $P = 0.004$; core-area model: $F = 3.2$, $P = 0.005$). Overlap of RCW home-ranges during the winter season was lower for groups at low density than

for groups at medium or high density (Table 2, Fig. 3). Overlap of RCW core-areas during the post-fledging season was less at low and medium density conditions than at high density conditions (Fig. 3).

## Space use and reproduction

The interaction between density condition and home-range size had a significant effect on clutch size (home-range model: $F = 3.6$, $P = 0.03$). Groups with larger home-ranges and at low densities had smaller clutches compared with groups at medium or high densities (Table 3). Additionally, RCW clutch sizes increased with home-range overlap at low densities more so than did clutch sizes of groups under medium and high-density conditions (Table 3, Fig. 4). We did not detect significant relationships between RCW group size and clutch size (Table 3). Core-area size and overlap did not affect RCW clutch size (Supporting Information Table S2).

Across all three density conditions, nestling and fledgling production were inversely

**Table 1.** Mixed-effects ANOVA comparing Red-cockaded Woodpecker home-range and core-area size estimates among groups at low, medium and high densities on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the mean breeding season home-range and core-area sizes for groups at high density.

| Parameter | Home-range size | | Core-area size | |
|---|---|---|---|---|
| | β | 95% CI | β | 95% CI |
| (Intercept) | 65.572*** | 52.14–79.00 | 13.523*** | 10.06–16.99 |
| Year | | | | |
| 2014 | −10.388* | −20.31 to −0.46 | −1.512 | −4.10 to 1.07 |
| Site | | | | |
| Savannah River Site | −9.173 | −25.41 to 7.07 | −2.374 | −6.60 to 1.85 |
| Group size | 5.301* | 0.102–10.492 | 1.199 | −0.164 to 2.563 |
| Density | | | | |
| Low | 16.703* | 0.46–32.94 | 3.786* | 0.44–8.01 |
| Medium | −3.425 | −19.67 to 12.81 | −0.606 | −4.83 to 3.62 |
| Season | | | | |
| Fledging | 26.859*** | 14.658–39.061 | 8.672*** | 5.500–11.845 |
| Post-fledging | 19.512** | 7.310–31.713 | 7.624*** | 4.452–10.797 |
| Winter | 35.663*** | 23.462–47.865 | 10.987*** | 7.814–14.159 |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 2.** Mixed-effects ANOVA models comparing Red-cockaded Woodpecker home-range and core-area overlap estimates among groups in low, medium and high densities on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the mean breeding season home-range and core-area overlap for groups at high density.
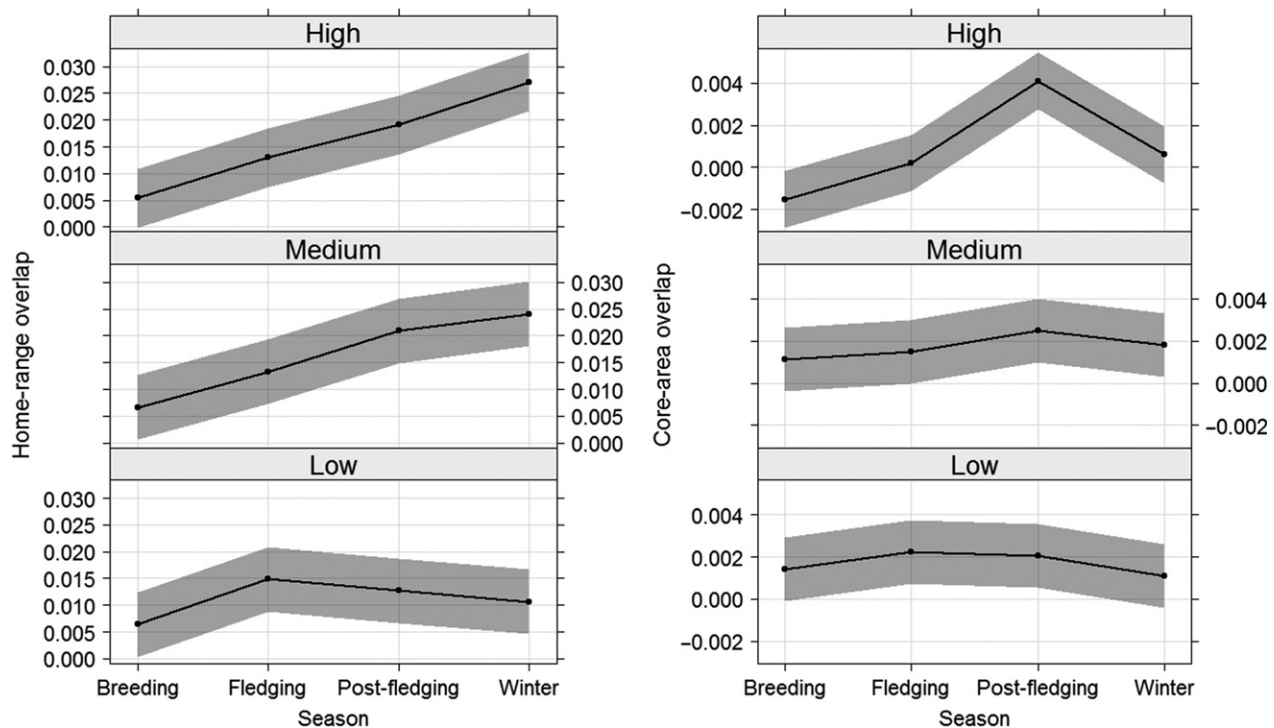
| Parameter | Home-range overlap | | Core-area overlap | |
|---|---|---|---|---|
| | β | 95% CI | β | 95% CI |
| (Intercept) | 0.014*** | 0.008–0.019 | 0.000 | −0.001 to 0.002 |
| Year | | | | |
| 2014 | −0.001 | −0.003 to 0.002 | 0.001** | 0.000–0.002 |
| Site | | | | |
| Savannah River Site | −0.011*** | −0.015 to −0.006 | −0.003*** | −0.005 to −0.002 |
| Group size | < 0.001 | −0.002 to 0.002 | < 0.001 | −0.001 to 0.001 |
| Density | | | | |
| Low | 0.000 | −0.008 to 0.009 | 0.003* | 0.001–0.005 |
| Medium | 0.000 | −0.008 to 0.009 | 0.002* | 0.000–0.005 |
| Season | | | | |
| Fledging | 0.008** | 0.002–0.013 | 0.002* | 0.000–0.003 |
| Post-fledging | 0.014*** | 0.008–0.019 | 0.006*** | 0.004–0.007 |
| Winter | 0.022*** | 0.016–0.027 | 0.002** | 0.001–0.004 |
| Density: Season | | | | |
| Low: Fledging | 0.001 | −0.008 to 0.009 | −0.001 | −0.003 to 0.002 |
| Medium: Fledging | −0.001 | −0.010 to 0.008 | −0.001 | −0.004 to 0.001 |
| Low: Post-fledging | −0.007 | −0.016 to 0.001 | −0.005*** | −0.007 to −0.003 |
| Medium: Post-fledging | 0.001 | −0.008 to 0.009 | −0.004** | −0.007 to −0.002 |
| Low: Winter | −0.017*** | −0.026 to −0.009 | −0.002 | −0.005 to 0.000 |
| Medium: Winter | −0.004 | −0.013 to 0.004 | −0.001 | −0.004 to 0.001 |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

associated with home-range overlap (Table 3, Fig. 5). The interaction between home-range overlap and neighbouring group density condition did not have a significant effect on nestling production or fledgling production (Table 3). Fledgling production increased slightly with home-

**Figure 3.** Relationships between Red-cockaded Woodpecker home-range and core-area overlap and season at low, medium and high group densities. Black circles connected by trend lines represent mean size estimates and grey bands represent 95% confidence intervals.

**Table 3.** Mixed-effects linear regression modelling variation in Red-cockaded Woodpecker 5-year mean fitness metrics (clutch size, nestling production and fledgling production) in response to group home-range sizes, overlap, density condition and group size for neighbouring woodpecker groups on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the 5-year mean clutch size, nestling production and fledgling production for groups at high density.

| | Clutch size | | Nestling production | | Fledgling production | |
|---|---|---|---|---|---|---|
| | β | se | β | se | β | se |
| (Intercept) | 2.87*** | 0.32 | 1.22*** | 0.33 | 0.74* | 0.30 |
| Density | | | | | | |
|   Low | 0.13 | 0.26 | −0.92*** | 0.25 | −0.66** | 0.21 |
|   Medium | −0.37 | 0.19 | −0.51** | 0.19 | −0.38* | 0.16 |
| Size (ha) | 0.02 | 0.14 | 0.07 | 0.14 | 0.03 | 0.12 |
| Overlap | −0.19* | 0.09 | −0.37*** | 0.09 | −0.34*** | 0.08 |
| Group size | 0.20 | 0.11 | 0.42*** | 0.11 | 0.43*** | 0.10 |
| Density: Size | | | | | | |
|   Low: Size | −0.37* | 0.18 | 0.09 | 0.18 | 0.18 | 0.16 |
|   Medium: Size | 0.17 | 0.20 | 0.14 | 0.20 | 0.12 | 0.17 |
| Density: Overlap | | | | | | |
|   Low: Overlap | 0.74* | 0.31 | 0.16 | 0.31 | 0.15 | 0.27 |
|   Medium: Overlap | −0.34 | 0.25 | 0.19 | 0.25 | 0.41 | 0.21 |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

range overlap under medium-density conditions (Fig. 5). Across all density conditions, larger groups had greater nestling and fledgling production (Table 3). Home-range and core-area sizes did not affect RCW nestling production or fledgling production (Tables 3 & S2).
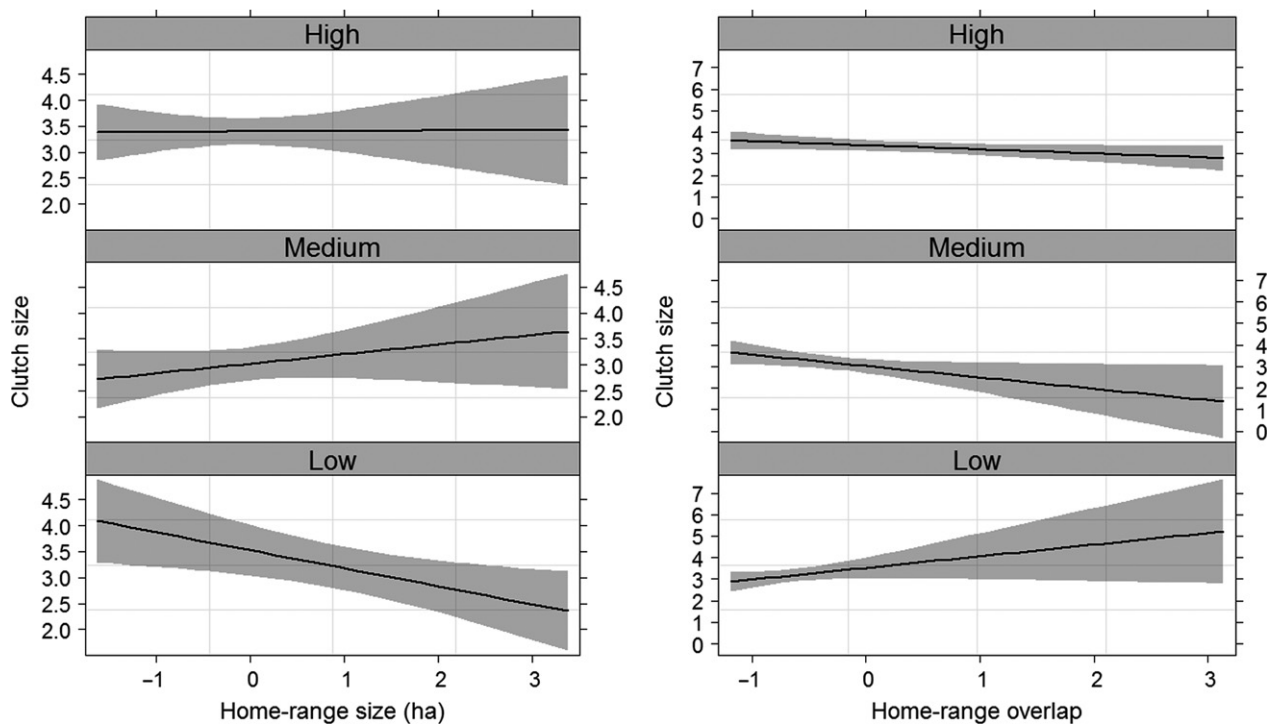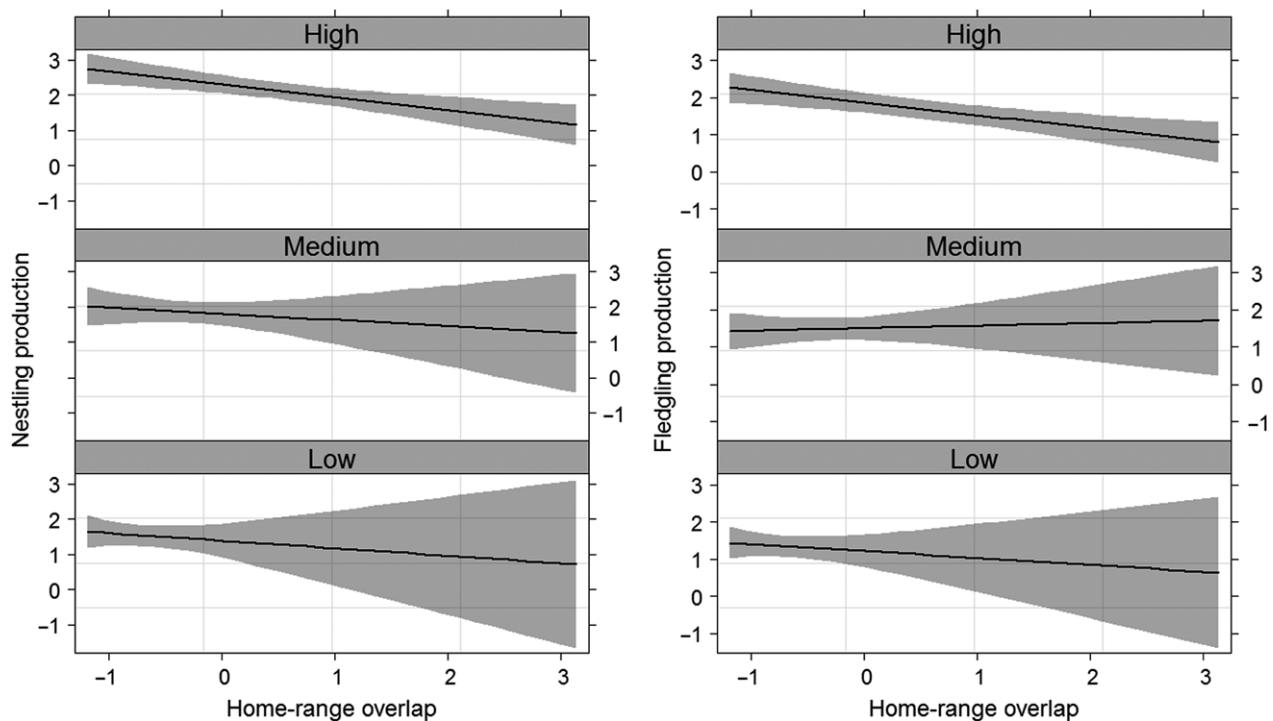
**Figure 4.** The relationship between home-range size and overlap and 5-year mean clutch size of Red-cockaded Woodpecker groups at low, medium and high group densities on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between 2013 and 2014. Black lines represent fitted interaction effects and grey bands represent 95% confidence intervals.

## DISCUSSION

Our analysis of space-use sharing and territorial behaviours suggests that RCW home-ranges are distinct from territories, which have been conflated in some previous RCW research. This is probably because most studies did not explicitly investigate frequencies of territorial behaviours or spatial overlap between neighbouring groups and thus were unable to distinguish territories from overlapping home-ranges (Leonard *et al.* 2008, Anich *et al.* 2009, Cooper *et al.* 2014). The fact that territorial interactions increased with density may help explain inconsistencies in the literature regarding relationships between RCW fitness and foraging habitat quality (Garabedian *et al.* 2014a). Territorial interactions can confound relationships between habitat quality and population density by influencing spacing patterns (Brown & Orians 1970), accessibility of limited resources including cavity trees and foraging habitat (Cox & McCormick 2016), and prospecting for potential dispersal destinations (Kesler & Walters 2012). With the rapid growth of many RCW populations over

recent decades, concomitant increases in territorial interactions between neighbouring groups could confound studies of resource selection used to develop standards of habitat quality (Walters 1991, James *et al.* 2001, Walters *et al.* 2002, Macey *et al.* 2016), minimum area requirements to support viable RCW populations (Reed *et al.* 1988, Zeigler & Walters 2014) and even retention of translocated RCWs in restored habitat (Cox & McCormick 2016).

Our results suggest habitat delineation for group-living territorial species may be improved by including a metric for intensity of space use within home-range boundaries. Most inferences about RCW home-range dynamics have been based on home-range sizes without reference to the intensity of use within home-range boundaries. The emphasis on home-range sizes stimulated use of polygon-based Thiessen partitions for critical habitat delineation, which are predicated on the assumption that neighbouring RCW groups equally partition space based on the distance between their cavity tree clusters (Schlicht *et al.* 2014). The fact that cavity tree clusters were not

**Figure 5.** Relationships between 5-year mean nestling and fledgling production and home-range overlap of Red-cockaded Woodpecker groups at low, medium and high group densities on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between 2013 and 2014. Black lines represent fitted lines and grey bands represent 95% confidence intervals.

centred in RCW home-ranges or territories suggests that critical habitat delineation based solely on the location of cavity trees does not accurately represent the habitat used most intensively by individual RCW groups (Cox & Engstrom 2001, Convery & Walters 2004, McKellar *et al.* 2014). Although the simplicity and limited data requirements for Thiessen partitions make them appealing for habitat protection, these qualities also render the technique misleading for spatially explicit habitat assessments at the individual level.

Our results suggest Thiessen foraging partitions are not reliable surrogates for RCW home-ranges, as has commonly been assumed when applied in studies of RCW home-range and habitat use (e.g. James *et al.* 1997, 2001, McKellar *et al.* 2014), because only core-areas are defended by RCWs. Thiessen foraging partitions appear to reflect the competitive processes that form RCW territories but not the home-ranges that overlap with neighbouring conspecifics (Schlicht *et al.* 2014). Our results suggest that limited territoriality outside exclusive core-areas associated with the cavity tree cluster is more common than active defence of the entire home-range (Nice 1941, Brown 1964,

Husak 2000). This may be attributable to RCWs exhibiting partial territoriality to minimize costs of territorial defence, defending only core-areas containing the cavity trees (DeLotelle & Epting 1988, Walters 1991). Defence of smaller, intensively used areas surrounding the cavity tree cluster suggests RCW populations are probably more tightly regulated by availability of cavity trees than availability of foraging habitat. Although mean home-range sizes decreased at all group densities in 2014 as compared with 2013, RCWs maintained stable core-areas throughout the study, suggesting the importance of exclusive access to habitat in core-areas is consistent over time because they contain the resource most limiting to RCW groups.

Based on our results, the intensity of use within overlapping areas of RCW home-ranges at high group density is more tightly linked to RCW fitness measures than is total area of overlap. Engstrom and Sanders (1997) observed that RCW fledgling production was greatest where home-ranges overlapped up to 30%, and RCWs routinely foraged within home-ranges and cavity tree clusters of neighbouring groups. Visual inspection of home-ranges from our study shows a high degree

of spatial overlap, supporting observations by Engstrom and Sanders (1997), but the relationships between overlap and fitness we observed differed because we did not assume use was constant in overlapping areas. Greater density of neighbouring groups may reduce fitness (i.e. clutch size, nestling and fledgling success) by increasing frequency of territorial interactions in overlapping areas, which probably reduces the time allocated to rearing young (Johnston *et al.* 2004). Competition for food before and during egg-laying can alter the amount of energy allocated to reproduction in many birds (Both *et al.* 2000, Brouwer *et al.* 2009). Female RCWs may be most affected prior to and during the breeding season, when energy demands are greatest (Daan *et al.* 1988, Jackson & Parris 1995).

Interestingly, larger RCW groups may offset fitness reductions associated with increased home-range overlap. For many group-living species, larger groups may have reduced fitness due to increased within-group competition for food and breeding positions (Solomon & Crist 2008, Maher & Burger 2011, Marjamäki *et al.* 2013). The positive relationships between RCW group size and fitness observed in this study can be attributed to increased provisioning rates in larger groups due to the presence of helper individuals, as observed in other group-breeding birds (e.g. Apostlebird *Struthidea cinera*; Woxvold & Magrath 2005). Increased frequency of provisioning in larger groups can lead to greater fledgling body mass, which increases winter survival when arthropod prey availability may be lower (Heinsohn 1991). In addition, during the post-fledging period, increased frequencies of within-group social interactions on the natal territory may improve foraging efficiency of juveniles (Weathers & Sullivan 1989).

Because relatively high densities and small home-ranges occurred on what is perceived as excellent (Wade Tract; Engstrom & Sanders 1997) as well as poor (Savannah River Site in the early 1990s; Franzreb 2006) quality habitat, our results are best interpreted as showing that RCW home-range dynamics respond to group density rather than foraging habitat quality. RCW group density is determined by the distribution of cavity trees, which is the primary factor influencing RCW space use once baseline foraging habitat requirements are satisfied (Hooper *et al.* 1982, Conner *et al.* 1999, Davenport *et al.* 2000), and we accounted for this

relationship in our study. In the absence of cavity trees, gradual improvements in other elements of RCW habitat over time would not be sufficient to drive the increases in RCW group density (Walters 1990, Hardesty *et al.* 1997, Carrie *et al.* 1998, Carlile *et al.* 2004) that explained home-range overlap in this study. Extensive home-range overlap observed in old-growth foraging habitat could be the result of higher RCW group density where cavity trees are locally dense rather than a relationship with foraging habitat quality (Engstrom & Sanders 1997). Hardwood mid-storey encroachment within the immediate vicinity of the cavity tree cluster can lead to cluster abandonment and therefore changes in RCW group density that influence space use (Conner & Rudolph 1989, Conner *et al.* 1999). Given that RCW group density did not change in our study due to cluster abandonment, it is unlikely habitat conditions confounded effects of group density on home-range overlap.

In the context of critical habitat delineation for RCW conservation, home-range overlap that increases with conspecific density does not satisfy assumptions of Thiessen partitions to delineate foraging habitat to individual RCW groups. Based on our results, continued use of Thiessen foraging partitions will benefit RCW populations with comprehensive habitat protection but managers should be aware that Thiessen partitions may overestimate the extent of territories and do not adequately account for increases in home-range overlap with conspecific density that can reduce RCW group fitness. We conclude that Thiessen partitions as currently applied represent a suitable method to protect critical habitat. However, they do not accurately delineate the space used by individual RCW groups and therefore could be problematic when used for spatially explicit habitat assessments for individual groups.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Annual core-area and home-range boundaries for Red-cockaded Woodpecker groups at low density on the Savannah River Site, South Carolina.

**Figure S2.** Annual core-use and home-range boundaries for Red-cockaded Woodpecker groups at medium density on the Savannah River Site, South Carolina.

**Figure S3.** Annual core-use and home-range boundaries for Red-cockaded Woodpecker groups at high density on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina.

**Table S1.** Red-cockaded Woodpecker home-range behaviours observed for groups in low, medium and high-density conditions on the Savannah River Site (SRS) and Carolina Sandhills National Wildlife Refuge (CSNWR), South Carolina, between April 2013 and March 2015.

**Table S2.** Mixed-effects linear regression modelling variation in Red-cockaded Woodpecker 5-year fitness metrics (clutch size, nestling production and fledgling production) in response to group core-area sizes, overlap, density condition and group size for neighbouring woodpecker groups on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015.