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The work reported here describes the project "Range-Wide Meta-Analysis of Red-Cockaded Woodpecker Foraging Habitat Suitability." This project was conducted under a cooperative agreement between the Engineer Research and Development Center - Construction Engineering Research Laboratory (ERDC-CERL) and The Curators of the University of Missouri. The primary objective of this project was to support conservation and recovery of a federally listed endangered avian species, the red-cockaded woodpecker (RCW; Picoides borealis). We aimed to identify the range of habitat conditions, as opposed to a single condition, that constitutes high-quality foraging habitat for RCWs, which will support recommendations for new RCW foraging habitat guidelines. This project has two components: (1) studies of the relationship between foraging habitat and RCW fitness across the species range, and (2) studies of foraging habitat selection by individual RCW groups on Eglin Air Force Base.

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RANGE-WIDE META-ANALYSIS OF RED-COCKADED WOODPECKER FORAGING HABITAT SUITABILITY

FINAL PROJECT REPORT

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EXECUTIVE SUMMARY

The work reported here describes the project "Range-Wide Meta-Analysis of Red-Cockaded Woodpecker Foraging Habitat Suitability." This project was conducted under a cooperative agreement between the Engineer Research and Development Center - Construction Engineering Research Laboratory (ERDC-CERL) and The Curators of the University of Missouri. The primary objective of this project was to support conservation and recovery of a federally listed endangered avian species, the red-cockaded woodpecker (RCW; *Picoides borealis*). We aimed to identify the range of habitat conditions, as opposed to a single condition, that constitutes high-quality foraging habitat for RCWs, which will support recommendations for new RCW foraging habitat guidelines. This project has two components: (1) studies of the relationship between foraging habitat and RCW fitness across the species range, and (2) studies of foraging habitat selection by individual RCW groups on Eglin Air Force Base.

Part 1: Range-wide variation in foraging habitat quality

We obtained RCW demographic data from the most recently available 5-year period from six military installations (Fort Benning, Fort Bragg, Fort Jackson, Fort Polk, Fort Stewart, and Marine Corps Base Camp Lejeune) and four United States Department of Agriculture National Forests (Apalachicola National Forest, Conecuh National Forest, Osceola National Forest, and Ouachita National Forest). We also obtained forest composition and ground cover data from the subset of populations for which standardized metrics were available (Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk).

Across all 10 populations, mean RCW group size ranged from 1.90-2.96 adults and mean annual fledgling production ranged from 0.77-1.79 fledglings. There was a general tendency for higher fledgling production at more northern and inland populations compared to more southern and coastal populations, but no clear geographic patterns emerged for group size.

For the five populations for which habitat data were available (Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk), we found considerable variation in mean habitat components on RCW territories. Habitat components fell outside of the bounds recommended in the RCW Recovery Plan (USFWS 2003) for certain habitat metrics. In particular, RCW territories tended to have higher basal area and densities of small pine trees (those with 10.2-25.4 cm [4-10 in] diameter at breast height) and lower percentages of herbaceous groundcover than was recommended in the Recovery Plan. In contrast, many territories were below the recommended maximum values for hardwood components, indicating that hardwoods have been managed to Recovery Plan specifications in most areas.

We generated territory quality scores from the RCW Foraging Habitat Matrix Application for the five populations with both demographic and habitat data (Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk). We found few associations between territory quality scores and RCW group size or fledgling production, indicating that the Foraging Matrix Application was not a strong predictor of RCW fitness on most territories. To further examine local relationships between habitat components and RCW fitness, we performed regression tree analyses for each of the five populations. Regression tree analysis allowed a visualization of the particular habitat components, and their values, that were associated with higher or lower group size or fledgling production separately for each population. Using the results of these analyses and the corresponding regression tree output, we were able to identify specific threshold values of habitat components that could lead to increased fitness at each population. Density of large pines and percentage herbaceous groundcover consistently emerged as variables affecting fitness, but their threshold values varied across populations. We were also able to identify some general areas for which Recovery Plan guidelines might be improved in order to fully capture the range of habitats where RCW groups are productive.

Part 2: Space use and resource selection at Eglin Air Force Base

For the second part of this project, we analyzed a dataset of follows of RCW groups at Eglin Air Force Base, Florida, that were performed in 2007 and 2008. Observers, equipped with global positioning system (GPS) units, followed groups of RCWs during early morning foraging bouts. This large dataset consisted of a total of 451 group follows at 97 individual RCW territories for a total of 37,109 GPS points (GPS locations were recorded approximately once each minute).

We found that groups traveled a maximum distance of 1,295 m (0.8 mi) from their territory center. Distance traveled tended to be longest in winter and shortest in spring, indicating that nesting may hinder large movements in spring and/or colder temperatures, and correspondingly lower insect activity, may require groups to forage more widely in winter. We found that the territory partitions used by managers to define RCW territories (i.e., 0.8 km [0.5 mi] Thiessen polygons) were generally effective at capturing RCW foraging activities. In other words, most groups stayed within their territory partition throughout the group follows, although there were several exceptional cases in which groups spent long periods of time outside of their partition. These exceptions tended to occur in winter (when movements were larger) and when territory partitions were smaller due to dense aggregation of territory centers.

We analyzed resource selection by comparing the habitat features of areas used by RCW groups to those of random, un-used areas. We found that RCW groups tended to select forest stands with higher densities of large pine trees (> 25.4 cm [10 in] diameter at breast height) and lower densities of small pine trees (10.2-25.4 cm [4-10 in] diameter at breast height). In contrast, resource selection was not as strongly associated with hardwood densities, RCW Foraging Matrix Application scores or Eglin Foraging Model scores. Further, we found that resource selection depended on both location within the territory and on group size. Groups were more selective when farther from their territory center, indicating that greater foraging rewards must be obtained at greater distances, in order to overcome the elevated costs of transit. Larger groups tended to be less selective than smaller groups for stands with higher large pine densities, perhaps indicating that the many ongoing social interactions in larger groups may hinder optimal habitat selection. However, the same was not true for selection against stands with more small pine trees: here, larger groups were more selective against this habitat feature. Overall, these results demonstrate that patterns of space use and resource selection can be influenced by social context and spatial factors in RCWs.

PART 1: RANGE-WIDE VARIATION IN FORAGING HABITAT QUALITY

1.1 BACKGROUND

The red-cockaded woodpecker is an endangered species endemic to the pine forests of the southeastern United States. Once perhaps the most common woodpecker in the region, today less than 1% of the bird's pre-colonial population size is thought to remain (Conner et al. 2001). Though widely scattered and highly fragmented, remaining RCW populations cover most of the species' historic range (Fig. 1). Three major factors contributed to drastic population declines of the past 500 years. First, loss of habitat through intense logging and land conversion reduced the species' preferred longleaf pine (*Pinus palustris*) forest habitat to only 3% of its original extent (Frost 1993). Second, loss of old pines degraded remaining habitat for RCWs, as RCWs are cooperative breeders that excavate roosting and nesting cavities only in mature live pines (Jackson et al. 1979). The abundance of such cavities has been shown to be a driver of RCW population processes (Walters et al. 1992). Third, fire suppression across the region further degraded habitat by allowing the development of dense hardwood midstories that shaded out the diverse ground cover that historically characterized these pine systems (Peet and Allard 1993).

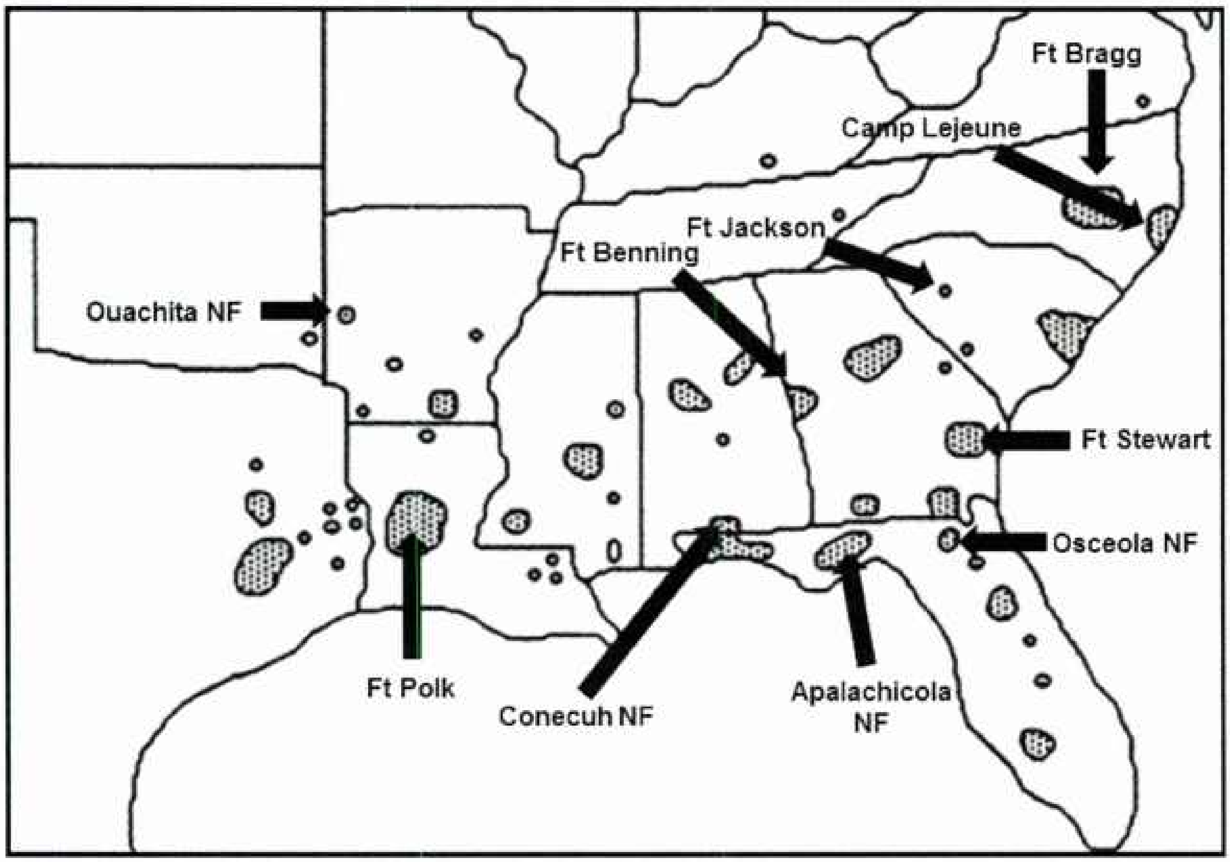

Figure 1. Current distribution of the red-cockaded woodpecker and sampling locations (marked with arrows) for analyses of demography and foraging habitat quality (map adapted from Conner et al. 2001).

Increased understanding of red-cockaded woodpecker ecology, greater emphasis on prescribed fire, and development of new management strategies such as construction of artificial nest and roost cavities have helped populations to increase (Walters 1991; Walters et al. 1992). Further studies in certain restored habitats indicated the impact of foraging habitat quality on RCW productivity. Larger group sizes, which generally indicated higher-quality territories (Butler and Tapp 2008), and greater fledging production were related to habitat features such as greater herbaceous groundcover, higher densities of large pines, and a reduced hardwood midstory (Hardesty et al. 1997; James et al. 1997, 2001; Walters et al. 2002). These findings were used to develop a new Red-Cockaded Woodpecker Recovery Plan (USFWS 2003) that included two sets of guidelines for managing foraging habitat: the recovery standard and the standard for managed stability. The recovery standard was recommended for use by federal agencies and state properties to facilitate recovery and increase population sizes. The standard for managed stability, on the other hand, was not designed to increase population size, but to be used when landowners could not manage to the recovery standard. Standards were based on pine and hardwood tree size and density and extent and composition of ground cover (USFWS 2003). In 2004, the U.S. Fish and Wildlife Service (USFWS), in collaboration with Environmental Systems Research Institute, Inc. (Redlands, CA), Fort Bragg, and the U.S. Army Environmental Center, developed the RCW Foraging Matrix Application to evaluate conditions based on the foraging habitat criteria in the recovery plan and produce scores based on the recovery standard and standard for managed stability. In recent years, the RCW Matrix Application has been updated and enhanced by Intergraph Corporation. Based on the recovery plan's criteria for good-quality foraging habitat, and expert opinion used to weight foraging habitat metrics, the RCW Matrix Application incorporates spatially-explicit forest stand data and territory locations to produce quantitative assessments of stand-level and territory-level foraging habitat quality.

Red-cockaded woodpecker populations have since increased in a variety of fire-maintained areas, but many of these areas differ in attributes such as pine density, abundance of hardwoods, and ground cover condition. Due to their protected status, RCWs have been intensely monitored at many locations. In particular, U.S. military installations have been instrumental in RCW monitoring and recovery, due to their intensive habitat monitoring and restoration efforts, large area, and the fact that they encompass some of the last remaining longleaf pine habitats. United States National Forests have also played an important role in monitoring of RCW populations (USFWS 2003). Combined, these data provide a unique opportunity to examine range-wide variation in foraging habitat quality and the effectiveness of the early foraging habitat guidelines in increasing RCW group sizes and fledgling production. We first summarize range-wide variation in RCW fitness components (group size and fledgling production) and foraging habitat metrics. We then test the performance of the RCW Foraging Matrix Application by relating RCW Matrix scores to RCW fitness. Finally, we evaluate range-wide variation in foraging habitat quality by relating RCW fitness to foraging habitat metrics through regression tree analyses that identify site-specific factors, and management thresholds, which are closely related to group size and reproduction.

1.2 METHODS

We collected RCW demographic data from two military installations, including Fort Bragg and Marine Corps Base Camp Lejeune (MCBCL), and we received data from an additional four military installations and four United States Department of Agriculture National Forests (NF), including Fort Jackson, Fort Benning, Fort Stewart, Fort Polk, Apalachicola NF, Osceola NF, Conecuh NF, and Ouachita NF (Table 1). Red-cockaded woodpecker group size and fledgling production were monitored for at least five consecutive years at each site. We also received forest composition and ground cover data from the subset of sites for which standardized metrics were available (Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk). Sites ranged from Florida to North Carolina and west to Louisiana and Arkansas, covering much of the species' current distribution across the Coastal Plain and Piedmont regions of the southeastern USA (Fig. 1). Eastern sites were dominated by longleaf pine and some hardwoods (mostly oaks, *Quercus* spp.), whereas central and western sites tended to be characterized by higher densities of loblolly (*P. taeda*) and shortleaf pine (*P. echinata*), with some slash pine (*P. eliottii*). Groundcover was composed mainly of wiregrasses (*Aristida stricta* and *A. beyrichiana*) at eastern sites and bluestem grasses (*Andropogon* and *Schizachyrium* spp.) at western sites (Conner et al. 2001). Each study site was represented by a contiguous population of RCWs with the exception of Fort Polk, which included two populations separated by approximately 30 km (19 mi). Data from Fort Polk populations were pooled because preliminary analyses indicated that they were similar in habitat (see "Installation Specific Results and Recommendations" for further discussion). Our analysis included a total of 1,944 active RCW territories (Table 1).

Table 1. Study sites used in analyses of foraging habitat quality for the red-cockaded woodpecker (RCW) between 2007 and 2012. Available territories were defined as those occupied by at least one RCW in at least one year of the study period, and area was calculated as the area including all RCW territories at a site (see Methods).

Site	Location	Ecoregion	Available territories	Area, ha (ac)
Fort Bragg	NC (79.30°E, 35.11°N)	Sandhills	391	37,000 (91,000)
MCBCL	NC (77.34°E, 34.59°N)	Atlantic Coastal Plain	94	8,000 (20,000)
Fort Jackson	SC (80.82°E, 34.04°N)	Sandhills	44	5,000 (12,000)
Fort Benning	GA (84.97°E, 32.37°N)	Sandhills	376	36,000 (89,000)
Fort Stewart	GA (81.61°E, 31.88°N)	Southern Coastal Plain	366	38,000 (94,000)
Apalachicola NF	FL (84.67°E, 30.24°N)	Eastern Gulf Coastal Plain	312	32,000 (79,000)
Osceola NF	FL (82.32°E, 30.29°N)	Atlantic Coastal Plain	149	15,000 (37,000)
Conecuh NF	AL (86.64°E, 31.10°N)	Eastern Gulf Coastal Plain	43	4,000 (10,000)
Fort Polk	LA (93.08°E, 31.07°N)	Western Gulf Coastal Plain	106	9,000 (22,000)
Ouachita NF	AR (94.25°E, 34.50°N)	Eastern Gulf Coastal Plain	63	7,000 (20,000)

Group size and fledgling production

Red-cockaded woodpeckers are non-migratory and occupy year-round territories as solitary males, pairs, or cooperatively breeding groups (Walters et al. 1988, 1992; Jackson 1994). Pairs and groups typically forage together during the day and throughout their multi-use territory (Conner et al. 2001). Territories are centered on a cluster of trees with nesting and roosting cavities (Lennartz et al. 1987), and breeding pairs can be assisted by up to five helpers, which are typically delayed dispersers fledged during previous breeding seasons (Conner et al. 2001).

Two metrics were used to reflect the suitability and productivity of RCW territories: group size and the number of fledglings produced. Higher-quality territories have been shown to host larger groups of birds (Butler and Tapp 2008), and reproduction is thought to be associated with territory quality, although it has also been associated with other factors, including the age of dominant birds and number of helpers (Heppell et al. 1994; Conner et al. 2001). Group size and fledgling production at each territory were recorded at each study site during the breeding season (April-June). The vast majority of birds were marked with individual-specific color band combinations due to intensive capture and banding of adults and nestlings each year. Group size was determined by repeated visits to each territory and identification of color-banded individuals foraging together. We used the maximum number of adults observed during the breeding period on a territory as the group size for that territory. Nest fate and number of fledglings were determined by repeated visits during the incubation and nesting periods, until a nest failed or young successfully fledged. We used number of young fledged, which we term *fledgling production*, as our measure of reproductive success. For groups that attempted to re-nest following a failed attempt, we used the number of fledglings of their final attempt. For groups that attempted a second nest following a successful first nest, we used the number of fledglings of their first nest. For each site, we used data from the most recent five consecutive years of study available, including 2007-2011 ($n = 3$ sites) or 2008-2012 ($n = 7$ sites). We calculated mean group size and mean fledgling production for each available territory during the five-year period, where an available territory was defined as one that was occupied by at least one adult RCW in at least one of the years of study (see also below for territory delineation). Years when no adults were present on a territory were not included in the calculation of mean group size and mean fledgling production.

Foraging habitat metrics and RCW territories

Standardized forest inventory data were available from five study sites, as required by the USFWS Recovery Guidelines (USFWS 2003). Data were provided to us in the form of forest stand geodatabases (spatial and quantitative stand representations) from the forestry divisions at Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk. Habitat metrics used in our study included number of stems and basal area of pines or hardwoods in three different size classes (10.2-25.4 cm [4-10 in] diameter at breast height [dbh], 25.4-35 [10-14 in] cm dbh, and > 35 cm [14 in] dbh), percent of herbaceous groundcover, and an index of hardwood midstory (Table 2). Note that the RCW Recovery Plan listed nine criteria for good quality foraging habitat (USFWS 2003), and six of these criteria relate directly to foraging habitat metrics used in our study (Table 2).

The RCW cavity tree locations for each territory were provided from endangered species biologists at the above five sites. We defined RCW territories by first calculating territory centers as the arithmetic mean of cluster tree coordinates, and we used ArcMap version 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) to create circular partitions of 0.8 km (0.5 mi) radii around each territory center. When two or more circular partitions would otherwise overlap, we used thiessen polygons to delineate territories used by each group. This method of habitat partitioning has been found to reasonably reflect the actual home range used by RCW groups (Convery and Walters 2004) and is the current method advocated by the U.S. Fish and Wildlife Service and used in the RCW Matrix to define RCW territories (see below). Hereafter, we use the term "territory" to represent the habitat area within partitions.

Table 2. Six criteria used by the U.S. Fish and Wildlife Service to define good quality foraging habitat for the red-cockaded woodpecker (USFWS 2003) and the corresponding habitat metrics evaluated in our study. Also included are seven additional habitat metrics used in our analyses that do not correspond directly to listed criteria.

Criteria for good quality foraging habitat	**Foraging habitat metric**
(1) There are 45 or more stems/ha (18 or more stems/ac) of pines that are > 60 years in age and > 35 cm (14 in) dbh. Minimum basal area for these pines is 4.6 m^2/ha (20 ft^2/ac).	Mean number of pine stems/ha > 35 cm (14 in) dbh (PTPA.35). Mean pine basal area/ha > 35 cm (14 in) dbh (PBA.35).
(2) Basal area of pines 25.4-35 cm (10-14 in) dbh is between 0 and 9.2 m^2/ha (0 and 40 ft^2/ac).	Mean pine basal area/ha 25.4-35 cm (10-14 in) dbh (PBA.25.35).
(3) Basal area of pines < 25.4 cm (14 in) dbh is below 2.3 m^2/ha (10 ft^2/ac) and below 50 stems/ha (20 stems/ac).	Mean pine basal area/ha 10.2-25.4 cm (4-10 in) dbh (PBA.10.25). Mean number of pine stems/ha 10.2-25.4 cm (4-10 in) dbh (PTPA.10.25).
(4) Basal area of all pines > 25.4 cm (10 in) dbh is at least 9.2 m^2/ha (40 ft^2/ac). That is, the minimum basal area for pines in categories (1) and (2) above is 9.2 m^2/ha (40 ft^2/ac).	Mean pine basal area/ha > 25.4 cm (10 in) dbh (PBA.25).
(5) Groundcovers of native bunchgrass and/or other native, fire-tolerant, fire-dependent herbs total 40 percent or more of ground and midstory plants and are dense enough to carry growing season fire at least once every 5 years.	Percent herbaceous groundcover (HERB).
(6) No hardwood midstory exists, or if a hardwood midstory is present it is sparse and less than 2.1 m (7 ft) in height.	Index of hardwood midstory[a] (HWDMID).
Other	Mean number of pine stems/ha 25.4-35 cm (10-14 in) dbh (PTPA.25.35). Mean number of hardwood stems/ha 10.2-25.4 cm (4-10 in) dbh (HTPA.10.25). Mean number of hardwood stems/ha 25.4-35 cm (10-14 in) dbh (HTPA.25.35). Mean number of hardwood stems/ha > 35 cm (14 in) dbh (HTPA.35). Mean hardwood basal area/ha 10.2-25.4 cm (4-10 in) dbh (HBA.10.25). Mean hardwood basal area /ha 25.4-35 cm (10-14 in) dbh (HBA.25.35). Mean hardwood basal area /ha > 35 cm (14 in) dbh (HBA.35).

[a] 1 = Low, Sparse; 2 = Low, Moderate; 3 = Low, Dense; 4 = Medium, Sparse; 5 = Tall, Sparse; 6 = Medium, Moderate; 7 = Tall, Moderate; 8 = Medium, Dense; 9 = Tall, Dense

RCW Foraging Matrix Application

We used the RCW Foraging Matrix Application (Intergraph Corporation, Huntsville, AL) to calculate habitat evaluation scores for territories at Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk. The application provides a numerical score for recovery standard (Rscore) and a pass/fail score for managed stability (Mscore). For the recovery standard, scores (0-5, with 5 being the highest) are first produced from individual stand-level evaluations of 12 characteristics which are then weighted by their presumed importance. Based on these scores, the total area of "good-quality foraging habitat" (GQFH) within the territory, pine within the territory, GQFH within 0.4 km (0.25 mi) of the territory center, and contiguous foraging habitat within the territory are each calculated, given a score (1-5, with 5 being the highest), and again weighted to produce an overall weighted score for the territory. Note that although stand-level scores range from 0-5 and territory scores from 1-5, overall territory Rscores tend to be lower (1.0-2.2 in our evaluations) because only stands that meet all standards set out in the Recovery Plan (i.e., receive a score of 5) are considered GQFH. The standard for managed stability is evaluated in a similar way, but with individual stands within a territory first scored as 0 (unsuitable) or 1 (suitable) for five characteristics, and based on these scores the total area of GQFH and pine basal area of pines > 25.4 cm (10 in) dbh within the territory are calculated and given a score of 0 or 1. The territory receives a final Mscore of 1 (pass) if both territory-level requirements are met.

Statistical analyses

We used multiple approaches to evaluate the relationship between RCW Matrix scores and RCW fitness metrics at the five sites where both RCW fitness and habitat metrics were available. First, we used linear regression to examine the relationship between RCW Matrix Rscores and (1) mean group size or (2) mean fledgling production on a territory during the five-year study period. Second, we used one-way ANOVA to examine the relationship between RCW Mscores and (1) mean group size or (2) mean fledgling production on a territory during the five-year study period. Third, we used linear regression to examine the relationship between the total number of hectares within a territory with Rscores greater than or equal to 4 and (1) mean group size or (2) mean fledgling production on a territory during the five-year study period.

We further assessed foraging habitat quality at each of the five sites with regression tree analyses (Breiman et al. 1984). In essence, the approach provided a way to use data from each site to identify site-specific conditions that were associated with higher and lower group sizes and fledgling production. Regression tree analysis is a non-parametric method based on recursive binary splitting of the original dataset into mutually exclusive groups by values of the predictor variables. Splits are identified so as to minimize the sum of squares of the dependent variable in each group, and the process is repeated such that the final output is a tree diagram with a root at the top containing the entire dataset and branches ending in nodes that contain average values of dependent variables, as predicted under chains of given conditions. This method was ideal for our analysis because it ultimately identifies breaks in patterns, or thresholds, at which ecological phenomena may occur, and the results can include complex interactions and nested relationships. Further, the approach accommodates large datasets, the data may be non-normally distributed and intercorrelated, and relationships between dependent and independent variables need not be linear (De'Ath and Fabricius 2000). After a full regression tree is grown to maximum size, it can be pruned back to an optimal size based on cross validation (Breiman et al. 1984). We used fifty 10-fold cross validations and the 1-SE rule to find the smallest tree with a relative error rate within one standard deviation of the minimum error rate (De'Ath and Fabricius 2000). We built two regression tree models for each site: one with RCW group size as the dependent variable, and the other with fledgling production as the dependent variable. Forest stand metrics and ground cover were used as independent variables. We used a global information system (GIS; ArcGIS, ESRI, Redlands, CA) to identify forest stands within RCW territories, and we calculated mean foraging habitat metrics by weighting forest metrics and ground cover values by the proportion of the area within the territory that they encompassed. Both types of models included the following 14 habitat metrics as independent variables: mean pine and hardwood densities (stems/hectare) and basal area (m^2/hectare) in each of three diameter at breast height size classes (10.2-25.4 cm [4-10 in], 25.4-35 cm [10-14 in], and > 35 cm [14 in] dbh), percent herbaceous groundcover, and an index of hardwood midstory. This includes all habitat metrics listed in Table 2 with the exception of PBA.25, which is simply the sum of PBA.25.35 and PBA.35. We built a total of 10 such models – one for each fitness measure (group size or fledgling production) at each of the five focal sites.

Within each of the aforementioned models, we also examined the top two competing "alternative splits" for each tree. In other words, if the first variable chosen in the splitting procedure was not included, we identified the next variable to be chosen and then the one to be chosen after that. Considering alternative splits can be useful for understanding associations and dependencies within the data that are not revealed by the final pruned tree (De'Ath and Fabricius 2000).

Finally, because managers are often interested in the amount of good quality foraging habitat required within each territory, rather than mean territory values (W. McDearman, pers. comm.), we built an additional five regression tree models with group size, and five with fledgling production, as dependent variables. We used the percentage of habitat within a territory that met the requirements for the primary split indicated from each of 10 trees described above. As an example, in an initial analysis we might build a regression tree for group size at Site A that indicated group sizes were larger with PTPA.35 > X. Then, using group size as the dependent variable and percentage of territory with PTPA.35 > X as the independent variable, we might find that territories with > Y% of the area having PTPA.35 > X had larger group sizes than those with < Y% of the area meeting that requirement. All statistical analyses were performed in R version 2.15.1 (R Development Core Team 2013), and we used the 'rpart' package for regression tree analysis.

1.3 GENERAL RESULTS

Group size and fledgling production

Mean group size per site ranged from 1.90-2.96 adults and did not show significant trends with latitude or longitude (Fig. 2; Group size vs latitude: $R^2 = 0.18$, $t_8 = 1.31$, $p = 0.228$; Group size vs longitude: $R^2 = 0.09$, $t_8 = -0.88$, $p = 0.405$). Mean annual fledgling production ranged from 0.77-1.79, and also did not show associations with latitude or longitude (Fig. 3; Fledgling production vs latitude: $R^2 = 0.29$, $t_8 = 1.82$, $p = 0.107$; Fledgling production vs longitude: $R^2 = 0.27$, $t_8 = -1.73$, $p = 0.122$). However, fledgling production was generally higher farther north and farther inland compared to more southern and coastal populations. Across all sites, mean territory group size explained about 18% of the variation in fledgling production ($R^2 = 0.18$, $t_{1777} = 19.9$, $p < 0.001$).

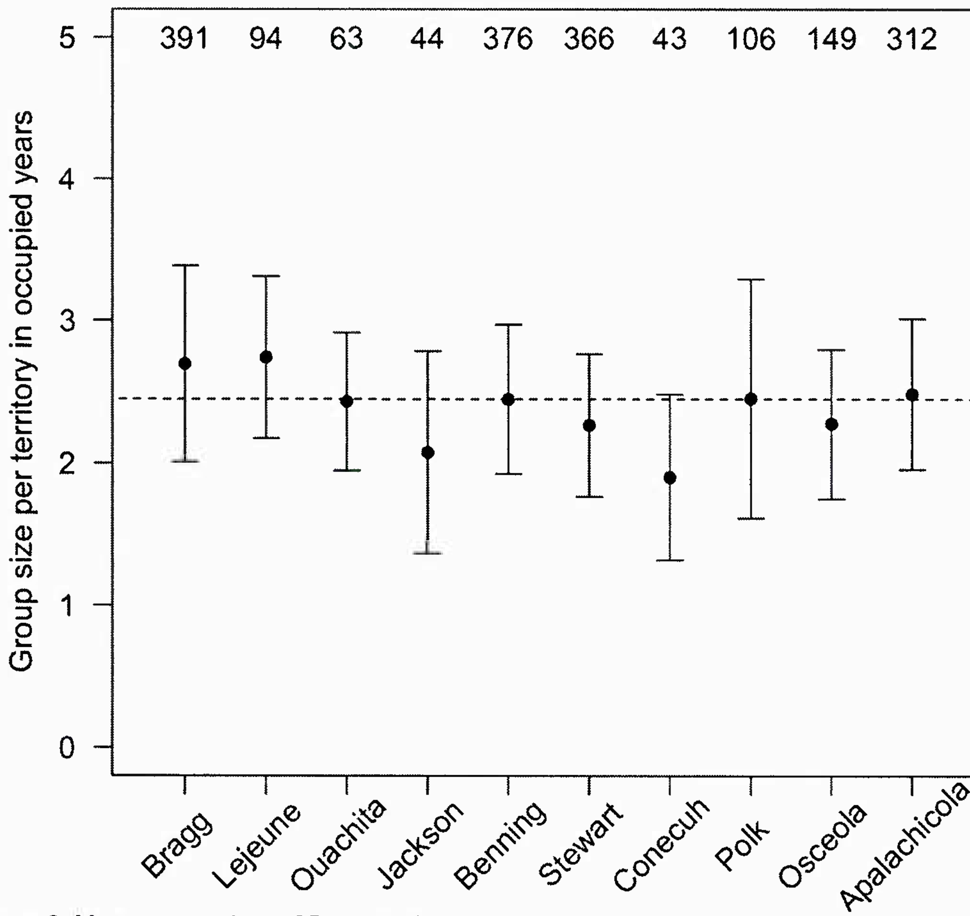

Figure 2. Mean group size ± SD per territory calculated using each year that at least one adult RCW was present on a territory between 2007 and 2012. Sample sizes are shown above each point and the dashed line indicates the overall mean. Sites are ordered by decreasing latitude.

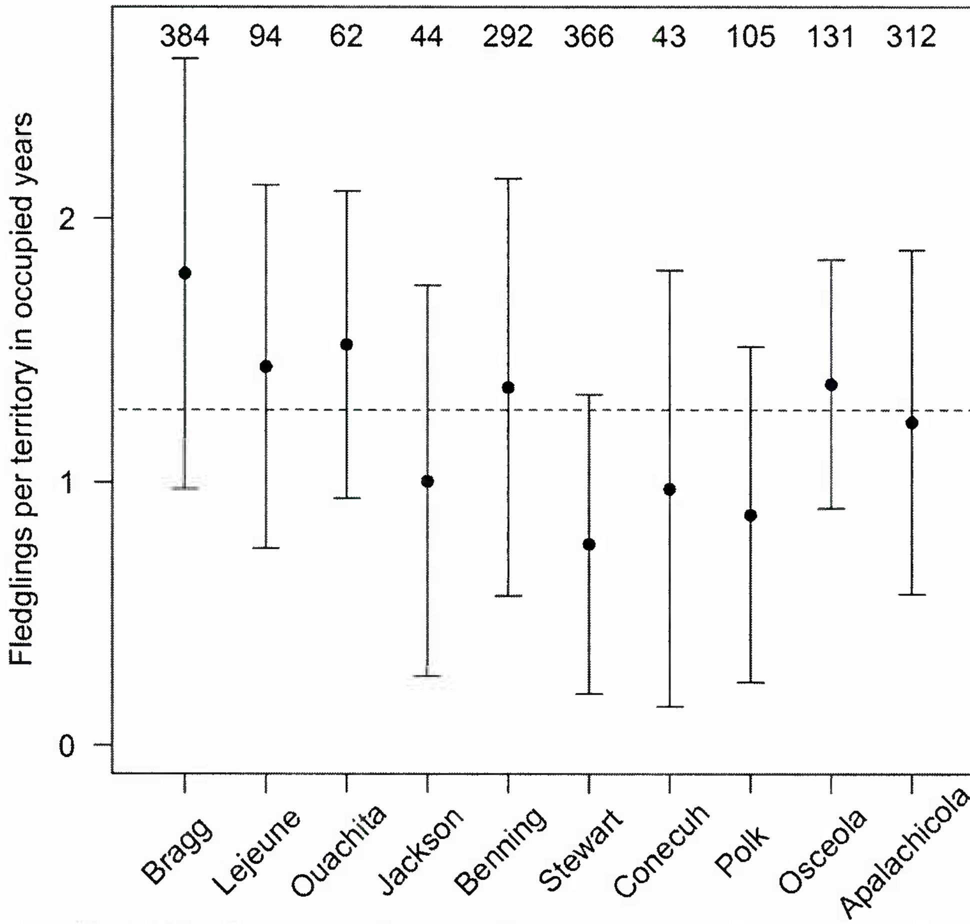

Figure 3. Mean annual fledging production per territory ± SD calculated using each year that at least one adult RCW was present on a territory between 2007 and 2012. Sample sizes are shown above each point and the dashed line indicates the overall mean. Sites are ordered by decreasing latitude.

Foraging habitat metrics

Forest metrics showed considerable variation across sites (Table 3, Figs 4 and 5), particularly with respect to herbaceous groundcover (Fig. 4g) and presence and density of hardwoods (Fig. 4h, Fig. 5b-g). Mean values of foraging habitat metrics on the most productive and least productive territories were generally similar to those on all territories combined at each site (Table 3). Notable were disparities in the proportion of habitat falling within the bounds of Recovery Plan guidelines for good quality habitat, which varied depending on the particular forest metric in question. For example, the vast majority of territories at all sites were below the recommended maximum of 9.2 m^2/ha (40 ft^2/ac) pine basal area for pines in the 25.4-35 cm (10-14 in) dbh class (Fig. 4c), but very few were below the recommended maximum of 2.3 m^2/ha (10 ft^2/ac) basal area with fewer than 50 stems/ha (20 stems/ac) for pines in the 10.2-25.4 cm (4-10 in) dbh class (Fig. 4d, e), and few were above the recommended minimum of 40% herbaceous groundcover (Fig. 4g).

Table 3. Values for habitat metrics on all territories and on the most productive (top 25% in terms of fledgling production) and least productive territories (bottom 25% in terms of fledgling production) at five military installations. Shown are the mean value ± SD. Basal area metrics are shown in m^2/ha (ft^2/ac in parentheses) and density metrics are shown in stems/ha (stems/ac in parentheses). See Table 2 for variable descriptions.

		Large pines		Medium pines		Small pines		Large hardwoods		Medium hardwoods		Small hardwoods			
Site		PBA.35	PTPA.35	PBA.25.35	PTPA.25.35	PBA.10.25	PTPA.10.25	HBA.35	HTPA.35	HBA.25.35	HTPA.25.35	HBA.10.25	HTPA.10.25	HWDMID	HERB
Fort Bragg	Top 25%	6.1±1.8 (26.6±7.8)	43.4±12.4 (17.6±5)	3.6±1.1 (15.7±4.8)	50.8±15.4 (20.6±6.2)	3.1±1.8 (13.5±7.8)	150±95.4 (60.7±38.6)	0.7±0.6 (3±2.6)	5±4.4 (2±1.8)	0.8±0.5 (3.5±2.2)	10.7±7.4 (4.3±3)	1.6±1 (7±4.4)	98.3±69.7 (39.8±28.2)	4.4 ±1.3	42.7 ±12.7
	Bottom 25%	6±1.7 (26.6±7.4)	43.2±12.2 (17.5±4.9)	3.6±1.4 (15.7±6.1)	49.2±19.2 (19.9±7.8)	2.6±1.5 (11.3±6.5)	131.9±77 (53.4±31.2)	0.8±0.9 (3.5±3.9)	5±5.2 (2±2.1)	0.7±0.6 (3±2.6)	10.3±9 (4.2±3.6)	1.5±1 (6.5±4.4)	96.3±59.6 (39±24.1)	4.6 ±1.1	39.8 ±10.4
	All	6±1.9 (26.6±8.3)	43.4±13 (17.6±5.3)	3.8±1.3 (16.6±5.7)	51.8±18.8 (21±7.6)	2.9±1.6 (12.6±7)	142.7±88.4 (57.7±35.8)	0.7±0.7 (3±3)	4.3±4.5 (1.7±1.8)	0.7±0.5 (3±2.2)	9.4±7.7 (3.8±3.1)	1.5±0.9 (6.5±3.9)	92.5±62.3 (37.4±25.2)	4.4 ±1.4	40.7 ±11.2
Fort Jackson	Top 25%	5.7±1.3 (24.8±5.7)	39.6±7.7 (16±3.1)	4.1±0.9 (17.9±3.9)	58.9±13.4 (23.8±5.4)	3.7±1.9 (16.1±8.3)	174.9±87.3 (70.8±35.3)	1.1±1.1 (4.8±4.8)	7.1±7.3 (2.9±3)	1.1±1.1 (4.8±4.8)	15.8±15.8 (6.4±6.4)	1.8±0.9 (7.8±3.9)	91.8±39 (37.2±15.8)	4.8 ±1.3	15.9 ±4.2
	Bottom 25%	5.4±1.1 (23.5±4.8)	38.3±7.5 (15.5±3)	3.8±1.1 (16.6±4.8)	55±16 (22.3±6.5)	4.2±1 (18.3±4.4)	219.7±30.1 (88.9±12.2)	0.8±0.8 (3.5±3.5)	5.1±5.4 (2.1±2.2)	0.9±0.8 (3.9±3.5)	13.3±12.5 (5.4±5.1)	1.8±0.8 (7.8±3.5)	97.8±42.2 (39.6±17.1)	6±1. 4	10.8 ±2.9
	All	5.5±1.2 (24±5.2)	37.5±8.1 (15.2±3.3)	3.6±1 (15.7±4.4)	51.9±14.4 (21±5.8)	3.7±1.5 (16.1±6.5)	184.2±70.8 (74.5±28.7)	1.4±1.2 (6.1±5.2)	8.8±7.3 (3.6±3)	1.3±1 (5.7±4.4)	19.5±13.9 (7.9±5.6)	2.2±1.2 (9.6±5.2)	118.2±63.1 (47.8±25.5)	5.6 ±1.4	13.6 ±4.2
Fort Benning	Top 25%	5.6±1.5 (24.4±6.5)	39.4±9.6 (15.9±3.9)	2.8±0.9 (12.2±3.9)	42.8±14.4 (17.3±5.8)	2±1.1 (8.7±4.8)	78.1±49.5 (31.6±20)	0.5±0.4 (2.2±1.7)	3.8±2.6 (1.5±1.1)	0.5±0.3 (2.2±1.3)	7.2±4.1 (2.9±1.7)	0.6±0.4 (2.6±1.7)	21.1±14.5 (8.5±5.9)	1.9 ±0.8	26.3 ±6.2
	Bottom 25%	5.3±2 (23.1±8.7)	37±12.6 (15±5.1)	2.9±1.2 (12.6±5.2)	44.4±17.8 (18±7.2)	2.5±1.6 (10.9±7)	97.2±65 (39.3±26.3)	0.5±0.3 (2.2±1.3)	3.4±2.2 (1.4±0.9)	0.4±0.3 (1.7±1.3)	7±5.3 (2.8±2.1)	0.5±0.3 (2.2±1.3)	17.5±12.7 (7.1±5.1)	2.3± 1	26 ±6.3
	All	5.5±1.5 (24±6.5)	38.7±9.9 (15.7±4)	2.9±1 (12.6±4.4)	43.6±15.6 (17.6±6.3)	2.1±1.5 (9.1±6.5)	81±78.2 (32.8±31.6)	0.5±0.4 (2.2±1.7)	3.6±2.5 (1.5±1)	0.4±0.9 (1.7±3.9)	7±13.2 (2.8±5.3)	0.5±1.3 (2.2±5.7)	19.5±79.4 (7.9±32.1)	2±1	26.5 ±5.9
Fort Stewart	Top 25%	6.8±2.5 (29.6±10.9)	48.8±17.4 (19.7±7)	4.4±1.5 (19.2±6.5)	61.2±20.7 (24.8±8.4)	2±1.3 (8.7±5.7)	87.8±57.2 (35.5±23.1)	0.6±0.4 (2.6±1.7)	3.9±2.7 (1.6±1.1)	0.7±0.4 (3±1.7)	10.6±6.2 (4.3±2.5)	1.3±0.8 (5.7±3.5)	66.9±46.3 (27.1±18.7)	2.7 ±1.3	14.4 ±5.4
	Bottom 25%	6.5±2.5 (28.3±10.9)	45.9±15.9 (18.6±6.4)	4±1.3 (17.4±5.7)	55±18.2 (22.3±7.4)	2.1±1.3 (9.1±5.7)	89.8±57.4 (36.3±23.2)	0.7±0.7 (3±3)	4.1±4.2 (1.7±1.7)	0.7±0.5 (3±2.2)	9.9±7.9 (4±3.2)	1.3±1 (5.7±4.4)	75.5±56.5 (30.6±22.9)	2.9 ±1.4	12.3 ±5.3
	All	6.5±2.4 (28.3±10.5)	45.8±16.4 (18.5±6.6)	4.1±1.4 (17.9±6.1)	46.2±19.6 (18.7±7.9)	2.1±1.3 (9.1±5.7)	88.7±56.4 (35.9±22.8)	0.7±0.7 (3±3)	4.3±4.1 (1.7±1.7)	0.7±0.5 (3±2.2)	10.6±7.8 (4.3±3.2)	1.3±0.9 (5.7±3.9)	72.7±52.6 (29.4±21.3)	2.8 ±1.4	13.4±6
Fort Polk	Top 25%	8±2.2 (34.8±9.6)	58.7±15.2 (23.8±6.2)	2.7±0.8 (11.7±3.5)	43.1±12.5 (17.4±5.1)	2±1.1 (8.7±4.8)	102.6±99 (41.5±40.1)	0.7±0.6 (3±2.6)	5.2±4.9 (2.1±2)	0.4±0.4 (1.7±1.7)	7.4±7.4 (3±3)	0.4±0.6 (1.7±2.6)	21.2±36.4 (8.6±14.7)	1.9 ±0.4	53.9 ±13.2
	Bottom 25%	8.1±2.2 (35.3±9.6)	58.4±16.9 (23.6±6.8)	2.7±1 (11.8±4.4)	43.2±16.4 (17.5±6.6)	2.5±1.5 (10.9±6.5)	131.7±99.5 (53.3±40.3)	0.6±0.6 (2.6±2.6)	4.8±5 (1.9±2)	0.4±0.4 (1.7±1.7)	6.6±6.5 (2.7±2.6)	0.4±0.3 (1.7±1.3)	14.2±10.2 (5.7±4.1)	1.8 ±0.4	50.7 ±5.6
	All	8±2.2 (34.8±9.6)	59.5±16.8 (24.1±6.8)	2.9±1.1 (12.6±4.8)	46.7±17.9 (18.9±7.2)	2.7±1.6 (11.8±7)	143±119.3 (57.9±48.3)	0.6±0.6 (2.6±2.6)	4.6±4.8 (1.9±1.9)	0.4±0.4 (1.7±1.7)	6.6±6.2 (2.7±.5)	0.4±0.4 (1.7±1.7)	16.1±21.8 (6.5±8.5)	1.8 ±0.4	52.6 ±9.8

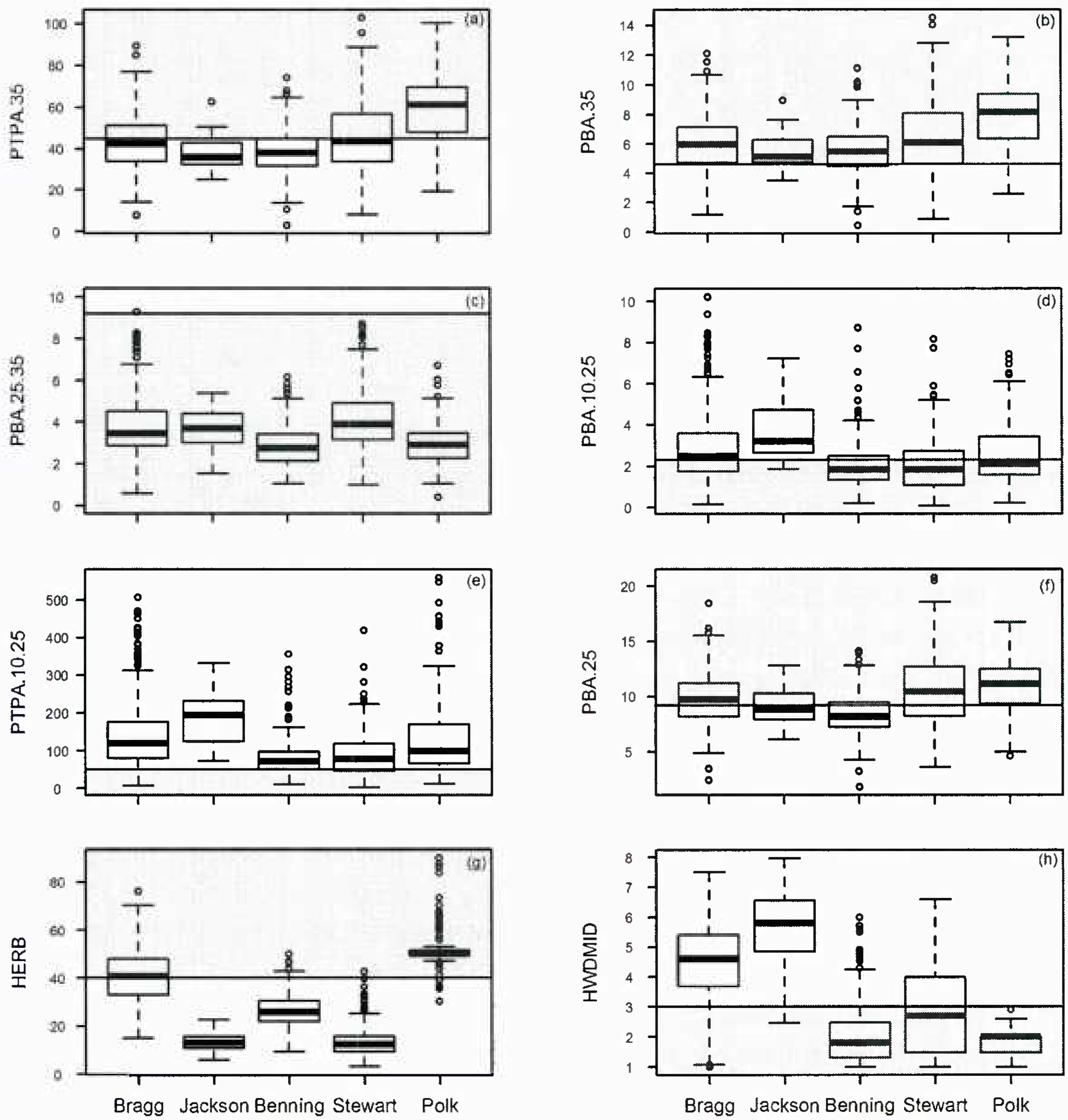

Figure 4. Variation in eight foraging habitat metrics used to define good quality foraging habitat for the red-cockaded woodpecker (Table 2, USFWS 2003). Shown are the median, interquartile range and outliers for habitat metrics on territories at each of five military installations where standardized forest inventory data were collected. Shaded areas indicate the range of values considered good quality foraging habitat according to the Recovery Plan guidelines. Units are m^2/ha for basal area and stems/ha for tree density. See Supplementary Figure S1 (Appendix) for an equivalent figure with metric values in ft^2/ac and stems/ac. See Table 2 for variable descriptions.

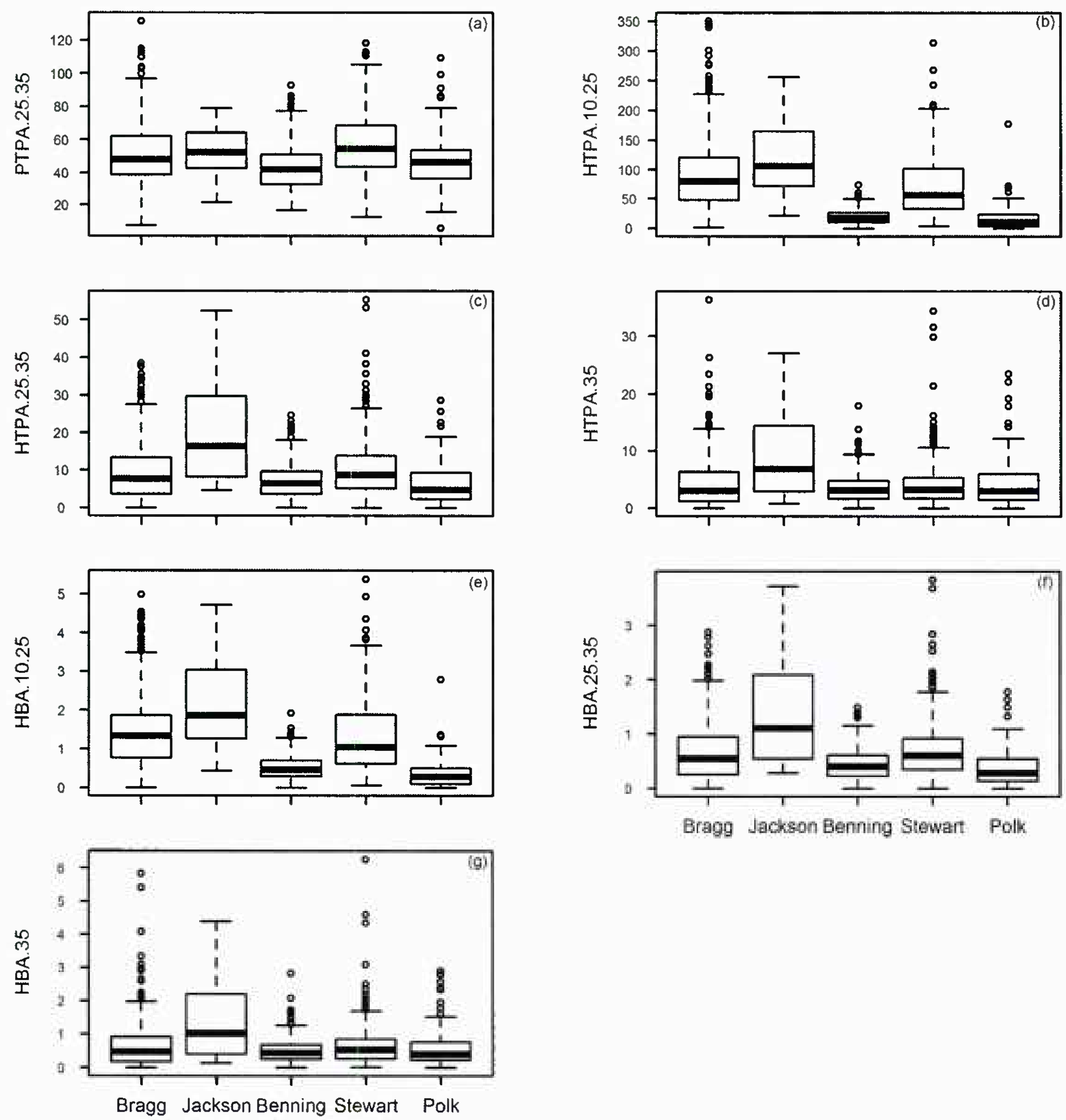

Figure 5. Variation in seven additional habitat metrics used in our study at each of five military installations where standardized forest inventory data were collected. Shown are the median, interquartile range and outliers for habitat metrics on territories at each of five military installations. Units are m^2/ha for basal area and stems/ha for tree density. See Supplementary Figure S2 (Appendix) for an equivalent figure with metric values in ft^2/ac and stems/ac. See Table 2 for variable descriptions.

RCW Matrix evaluations

Overall, RCW Matrix territory scores were not strong predictors of mean group size or fledgling production (Figs 6 and 7). However, territories with higher Rscores and those that had passing Mscores produced significantly more fledglings at Fort Bragg (Rscore: $R^2 = 0.01$, $t_{382} = 1.99$, $p = 0.047$; Mscore: $F_{1,382} = 6.40$, $p = 0.012$; Figs 6b, 7b), and territories with passing Mscores had significantly larger groups and produced significantly more fledglings at Fort Benning (Group size: $F_{1,302} = 7.42$, $p = 0.007$; Fledgling production: $F_{1,264} = 5.50$, $p = 0.020$; Fig.

7e, f). All other relationships between group size or fledgling production and Rscores or Mscores were non-significant.

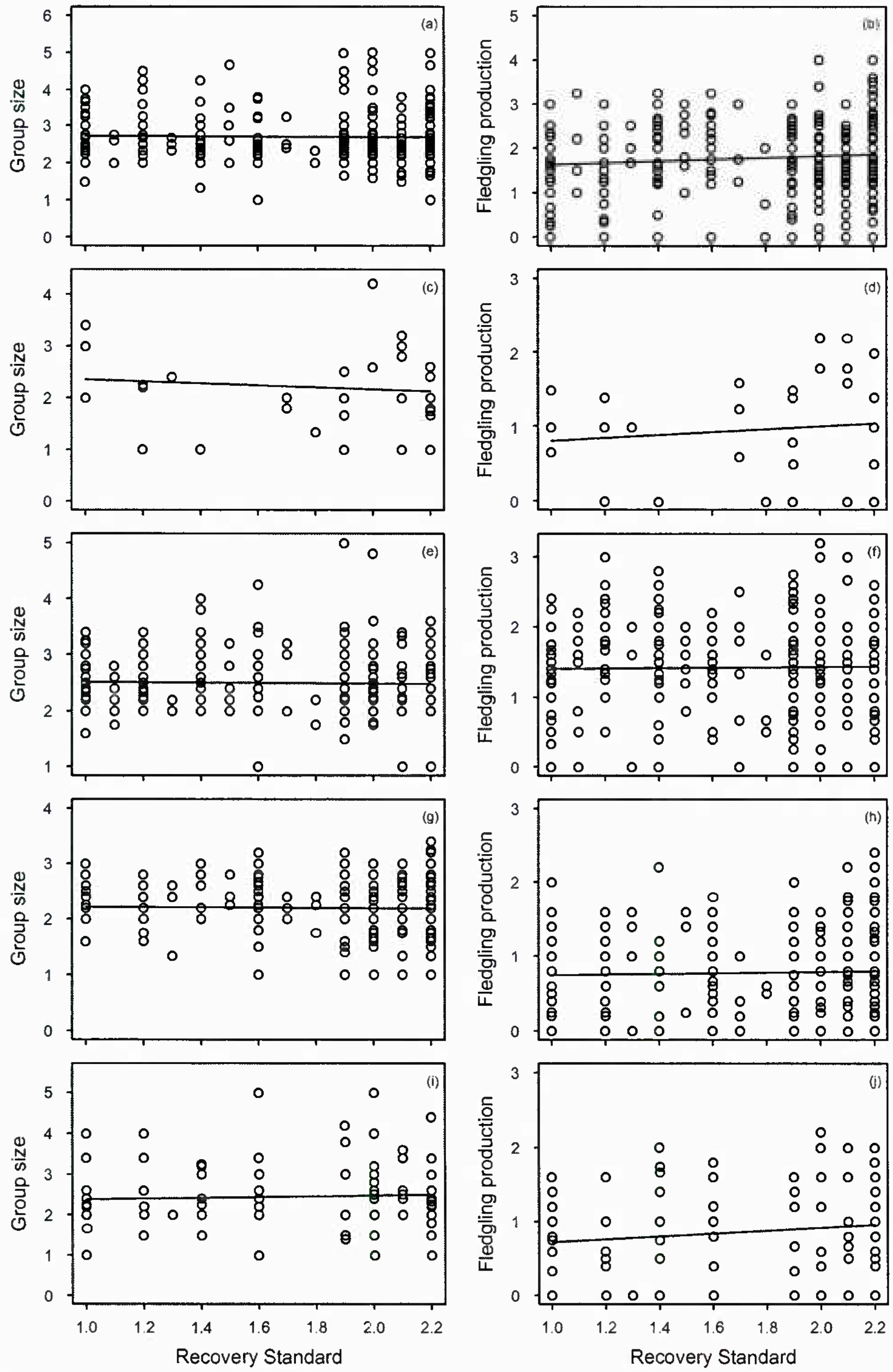

Figure 6. Relationship between mean group size or fledgling production and Recovery Standard score, as assessed by the RCW Foraging Matrix Application for individual territories at five military installations: (a), (b) Fort Bragg, (c), (d), Fort Jackson, (e), (f), Fort Benning, (g), (h), Fort Stewart, (i), (j), Fort Polk. Higher scores represent higher-quality foraging habitat, as assessed by the RCW Matrix.

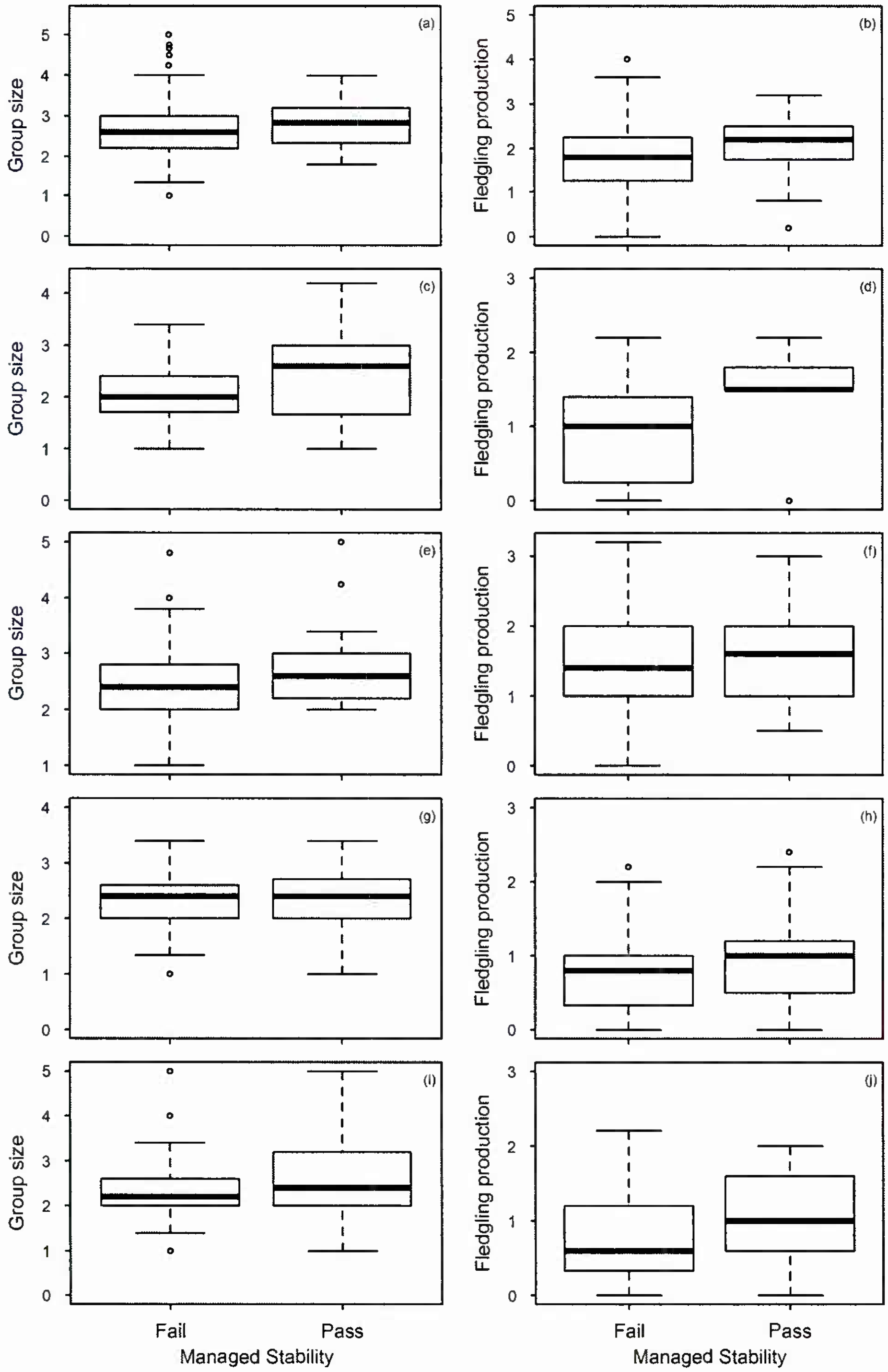

Figure 7. Distribution of group size or fledgling production on territories with a score of Fail or Pass for Managed Stability, as assessed by the RCW Foraging Matrix Application at five military installations: (a), (b) Fort Bragg, (c), (d), Fort Jackson, (e), (f), Fort Benning, (g), (h), Fort Stewart, (i), (j), Fort Polk.

Similarly, the number of hectares within a territory that received an Rscore of >= 4 was not strongly related to group size or fledgling production (Fig. 8), though this relationship was significant and positive for group size at Fort Jackson ($R^2 = 0.13$, $t_{31} = 2.15$, $p = 0.04$; Fig. 8c), for group size and fledgling production at Fort Benning (Group size: $R^2 = 0.03$, $t_{302} = 3.11$, $p = 0.002$; Fledgling production: $R^2 = 0.04$, $t_{264} = 3.43$, $p < 0.001$; Fig. 8e, f), and for fledgling production at Fort Stewart ($R^2 = 0.01$, $t_{345} = 2.11$, $p = 0.036$; Fig. 8h).

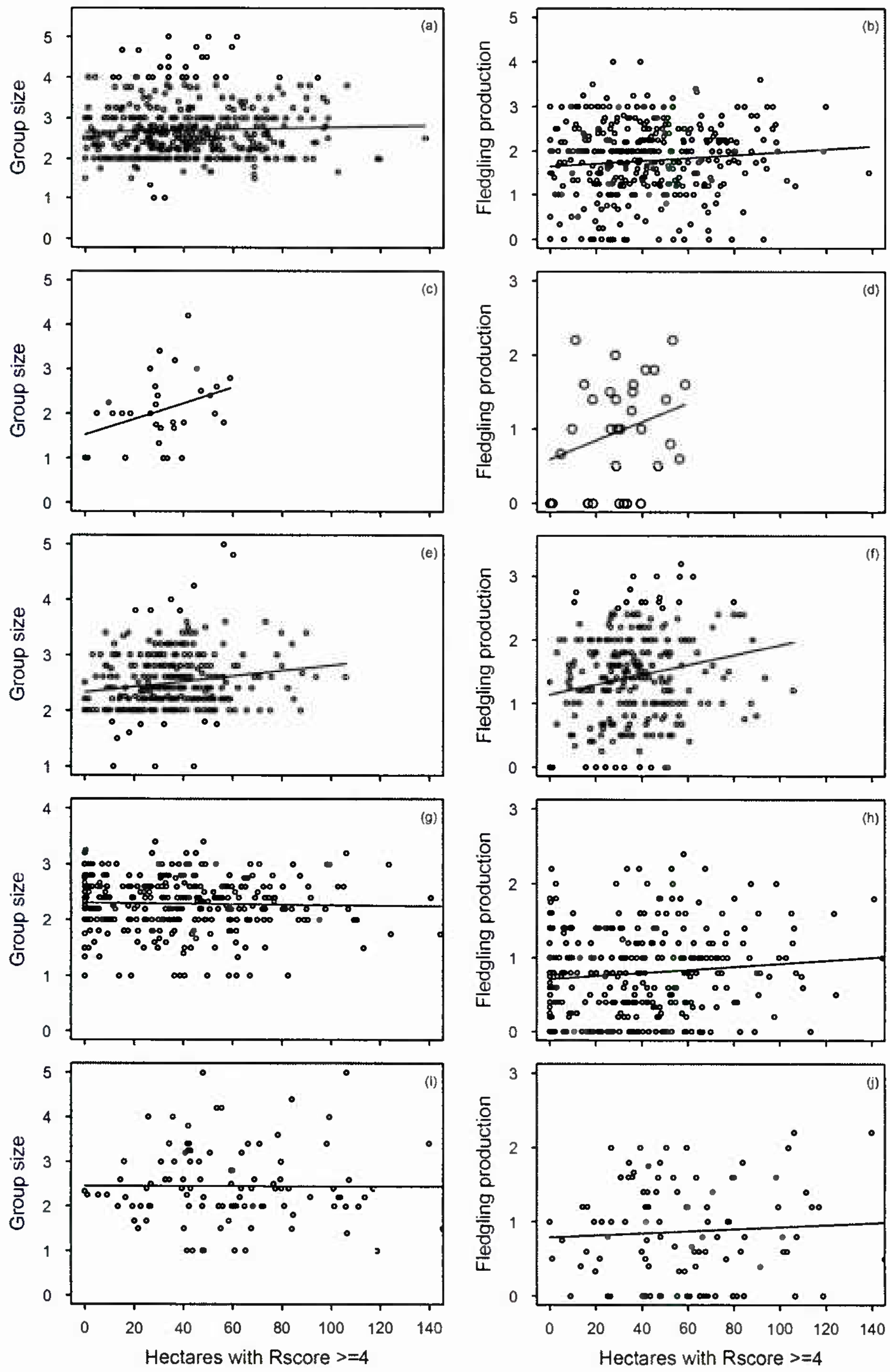

Figure 8. Relationship between mean group size or fledgling production and number of hectares with a Recovery Standard score >= 4 as assessed by the RCW Foraging Matrix Application for individual territories at five military installations: (a), (b) Fort Bragg, (c), (d), Fort Jackson, (e), (f), Fort Benning, (g), (h), Fort Stewart, (i), (j), Fort Polk. See Supplementary Figure S3 for an equivalent figure with values in acres.

Regression tree analyses

Our regression tree analyses revealed natural break-points in habitat metrics that were associated with higher or lower RCW fitness at each installation. The top habitat metrics selected by regression tree analyses, and their numerical value, differed among sites and between fitness measures (Table 4; Figs 9-18). Despite variation among sites, general trends were apparent when examining the three top habitat metrics identified in primary regression tree splits for group size and fledgling production at each site (Table 4). Greater stems/ha and basal area of large pines and higher levels of herbaceous groundcover were identified as important for RCW fitness across sites, and either higher or lower amounts of small pines were important, depending on the site. Herbaceous groundcover was most often associated with fledgling production, whereas pines were more often associated with group size (Table 4). We also identified thresholds in the percentage of habitat within a territory that met the requirements of the top primary split that were associated with higher or lower RCW fitness (Table 4 Footnotes). For example, territories with at least 87.9% of their area with basal area > 7.45 m^2/ha (32.5 ft^2/ac) of pines in the > 35 cm (14 in) dbh class at Fort Bragg were associated with larger group sizes compared to territories with less than 87.9% of their area meeting that requirement. In the following sections, we describe specific results and provide recommendations for each site.

Table 4. Summary of regression tree splits for the relationship between group size or fledgling production, and habitat metrics at five military installations. For each installation and for models with either group size (blue) or fledgling production (red) as the response variable, the three primary splits with the most support are shown. These include the primary split with the highest support (i.e., the one shown on regression tree diagrams, underlined) and two alternative primary splits. Secondary splits associated with the best primary splits, when present, are shown in brackets. All basal area and tree density values are shown in units of m^2/ha and stems/ha, respectively, but values in parentheses are in units of ft^2/ac and stems/ac. Split value inequalities (< or >=) show the direction that leads to larger group size or fledgling production. Also shown in black are the mean ± SD for each habitat metric at each site. Footnotes denote results of a second set of regression tree analyses in which the percentage of habitat within a territory that met the requirements of the top primary split was used as the independent variable, with group size or fledgling production as the dependent variable, and the threshold value of percentage habitat resulting in larger groups or greater fledgling production was determined.

	Large pines		Medium pines		Small pines		Large hardwoods		Medium hardwoods		Small hardwoods			
Site	**PBA.35**	**PTPA.35**	**PBA.25.35**	**PTPA.25.35**	**PBA.10.25**	**PTPA.10.25**	**HBA.35**	**HTPA.35**	**HBA.25.35**	**HTPA.25.35**	**HBA.10.25**	**HTPA.10.25**	**HWD MID**	**HERB**
Fort Bragg	>=7.45[a] (>=32.4)	>=50.22 (>=20.3)		[>=50.4] ([>=20.4])		<297.7 (<120.5)								
									>=0.46 (>=2)	>=5.23 (>=2.2)				>=59.19[b]
	6±1.9 (26.1±8.3)	43.4±13 (17.6±5.3)	3.8±1.3 (16.6±5.7)	51.8±18.8 (21±7.6)	2.9±1.6 (12.6±7)	142.7±88.4 (57.7±35.8)	0.7±0.7 (3±3)	4.3±4.5 (1.7±1.8)	0.7±0.5 (3±2.2)	9.4±7.7 (40.9±33.5)	1.5±0.9 (6.5±3.9)	92.5±62.3 (37.4±25.2)	4.4±1.4	40.7±11.2
Fort Jackson					<2.63 (<11.5)	<162.9 (<65.9)								>=14.28[c]
					<2.65 (<11.5)	<162.9 (<65.9) [<162.9] ([<65.9])								>=14.28[d]
	5.5±1.2 (24±5.2)	37.5±8.1 (15.2±3.3)	3.6±1 (15.7±4.4)	51.9±14.4 (21±5.8)	3.7±1.5 (16.1±6.5)	184.2±70.8 (74.5±28.7)	1.4±1.2 (6.1±5.2)	8.8±7.3 (3.6±3)	1.3±1 (5.7±4.4)	19.5±13.9 (7.9±5.6)	2.2±1.2 (9.6±5.2)	118.2±63.1 (47.8±25.5)	5.6±1.4	13.6±4.2
Fort Benning	>=5.48 (>=23.9)	>=44.7[e] (>=194.7)												>=27.42 (>=27.21)
	>=37 (>=13.4)	>=24.15[f] (>=9.8)			<1.61 (<7)									
	5.5±1.5 (24±6.5)	38.7±9.9 (15.7±4)	2.9±1 (12.6±4.4)	43.6±15.6 (17.6±6.3)	2.1±1.5 (9.1±6.5)	81±78.2 (32.8±31.6)	0.5±0.4 (2.2±1.7)	3.6±2.5 (1.5±1)	0.4±0.9 (1.7±3.9)	7±13.2 (2.8±5.3)	0.5±1.3 (2.2±5.7)	19.5±79.4 (7.9±32.1)	2±1	26.5±5.9
Fort Stewart	<9.16[g] (<39.9)				>=0.42 (>=0.17) [>=0.42] ([>=0.17])	>=17.4 (>=7)								
	[>=8.24] ([>=35.9])		>=6.72 (>=29.3)	>=93.53 (>=37.9)										>=14.4[h]
	6.5±2.4 (28.3±10.5)	45.8±16.4 (18.5±6.6)	4.1±1.4 (17.9±6.1)	46.2±19.6 (18.7±7.9)	2.1±1.3 (9.1±5.7)	88.7±56.4 (35.9±22.8)	0.7±0.7 (3±3)	4.3±4.1 (1.7±1.7)	0.7±0.5 (3±2.2)	10.6±7.8 (4.3±3.2)	1.3±0.9 (5.7±3.9)	72.7±52.6 (29.4±21.3)	2.8±1.4	13.4±6
Fort Polk	[<9.26] ([<40.3])				<2.01[i] (<8.7)	<95.89 (<38.8)						>=34.4 (>=13.9)		
					<2.25 (<9.8)	<111.1[j] (<45)						<8.44 (<3.4)		
	8±2.2	59.5±16.8	2.9±1.1	46.7±17.9	2.7±1.6	143±119.3	0.6±0.6	4.6±4.8	0.4±0.4	6.6±6.2	0.4±0.4	16.1±21.8	1.8±0.4	52.6±9.8

(34.8±9.6)	(24.1±6.8)	(12.6±4.8)	(18.9±7.2)	(11.8±7)	(57.9±48.3)	(2.6±2.6)	(1.9±1.9)	(1.7±1.7)	(2.7±2.5)	(1.7±1.7)	(6.5±8.8)

[a] > 87.9% of territory
[b] > 59.0% of territory
[c] > 7.5% of territory
[d] > 7.5% of territory
[e] > 36.7% of territory
[f] > 12.5% of territory
[g] > 75.5% of territory
[h] > 19.5% of territory
[i] > 25.4% of territory
[j] > 32.0% of territory

1.4 INSTALLATION-SPECIFIC RESULTS AND RECOMMENDATIONS

Fort Bragg

Regression tree analysis for Fort Bragg highlighted the importance of large pines for enhancing mean territory group size. Larger groups (mean of 2.9 adults) occurred on territories with greater than 7.5 m^2/ha (32.4 ft^2/ac) mean pine basal area of pines > 35 cm (14 in) dbh, in comparison to territories with less than 7.5 m^2/ha (32.4 ft^2/ac) pine basal area of pines > 35 cm (14 in) dbh (mean of 2.6 adults; Fig. 9). Further, of 85 territories with PBA.35 > 7.5 m^2/ha (32.4 ft^2/ac), those that also contained more than 50.4 pine stems/ha (20.4 stems/ac) of pines 25.4-35 cm (10-14 in) dbh had overall the largest groups (mean of 3.3 adults). Further analyses revealed that alternative thresholds occurred at 50.2 pine stems/ha (20.3 stems/ac) of pines > 35 cm (14 in) dbh and 297.7 pine stems/ha (120.5 stems/ac) of pines 10.2-25.4cm (4-10 in) dbh (Table 4). In other words, if PBA.35 was excluded from the analysis, the next-best regression tree splits identified territories containing more than 50.2 pine stems/ha (20.3 stems/ac) of large pines or fewer than 297.7 pine stems/ha (120.5 stems/ac) of small pines.

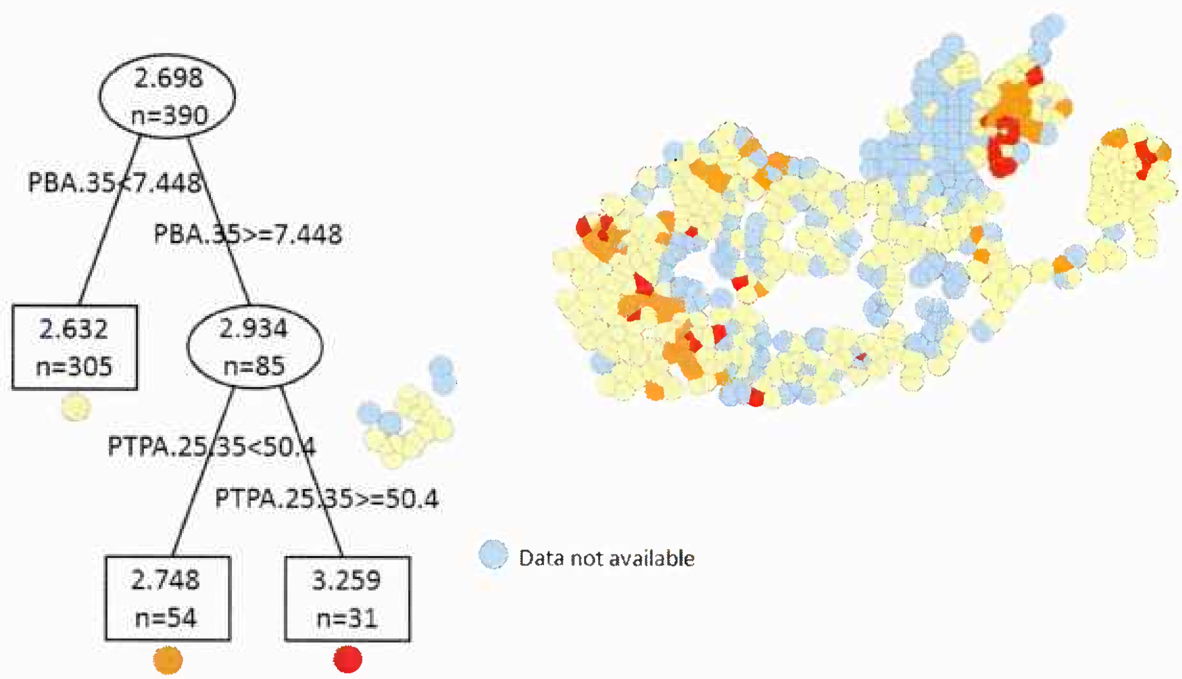

Figure 9. Left panel shows a pruned regression tree for evaluating the relationship between group size and 14 habitat metrics at Fort Bragg, NC. Each node is labeled with the mean group size (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Bragg with higher (red), intermediate (orange), and lower (yellow) group size as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from enhanced PBA.35 (> 7.448 m^2/ha or 32.4 ft^2/ac), whereas those shown in orange might benefit from enhanced PTPA.25.35 (> 50.4 stems/ha or 20.4 stems/ac).

The most influential habitat feature associated with fledgling production at Fort Bragg was herbaceous groundcover (Fig. 10). Territories with greater than 59% mean herbaceous groundcover produced more fledglings (mean of 2.4) than those with less than 59% mean herbaceous groundcover (mean of 1.8; Fig. 10). Interestingly, alternative thresholds occurred at

0.46 m^2/ha (2 ft^2/ac) basal area and 5.2 stems/ha (2.1 stems.ac) of hardwoods 25.4-35 cm (10-14 in) dbh (Table 4), indicating that the presence of some medium-sized hardwoods, rather than being harmful, may have a positive effect on fledgling production, as long as herbaceous groundcover is sufficient (e.g., Conner et al. 1996). We note that modest hardwood component represented by these threshold values is quite different from the dense hardwood midstory layers that are well-documented to have detrimental effects on RCWs (Conner and Rudolph 1989; Walters et al. 2002; Butler and Tappe 2008).

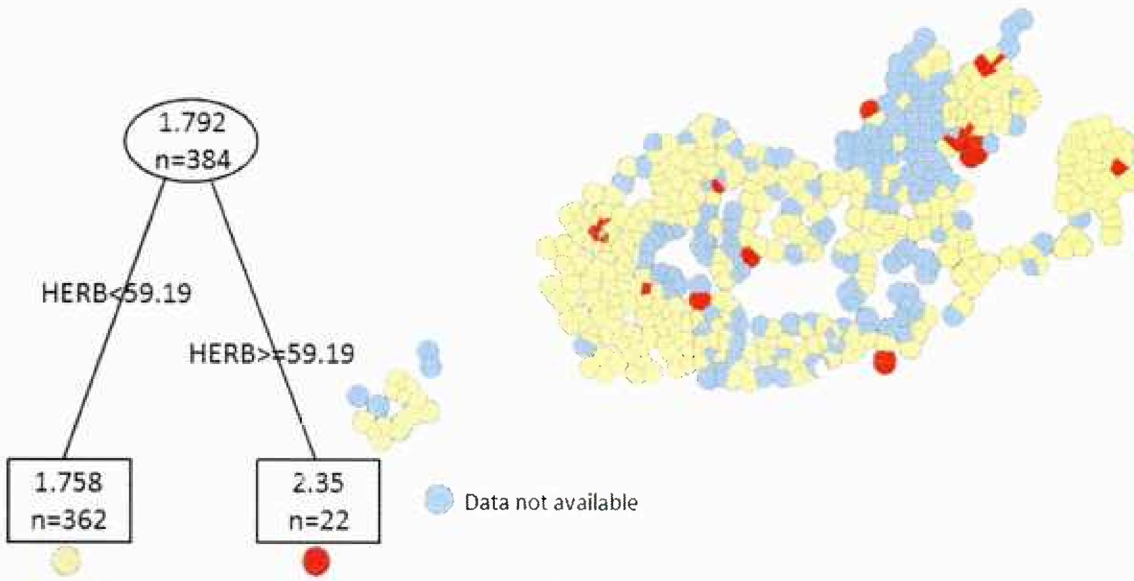

Figure 10. Left panel shows a pruned regression tree for evaluating the relationship between fledgling production and 14 habitat metrics at Fort Bragg, NC. Each node is labeled with the mean fledgling production (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Bragg with higher (red) and lower (yellow) fledgling production as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from additional herbaceous groundcover (> 59.19%).

The management implication of these results with respect to group size is that management should be geared toward increasing numbers and basal area of large pines, something that cannot easily be achieved on a short time-scale. Size is possibly a surrogate for age, as data on pine ages were not available to be included in the analysis, so positive results may be achieved simply by allowing forest stands to mature. Improving conditions for growth of larger trees (i.e., stand thinning) may also be effective. Our results emphasize the importance of maintaining the high-quality territories that already contain these features, as shown in orange and red in Figure 9. Providing extensive herbaceous groundcover, to maximize fledgling production, is more easily achievable through continuation of prescribed fire regimes. In fact, RCW territories on Fort Bragg already possess relatively high herbaceous groundcover (Fig. 4g) and also experience the highest mean fledging production among study sites (Fig. 3). However, few territories at Fort Bragg meet the threshold of 59% herbaceous groundcover (Fig. 10), and as noted in Table 4, the benefits of high herbaceous groundcover (>= 59%) are best achieved when covering at least 59% of a territory. Thus, increasing herbaceous groundcover on territories not currently meeting this threshold (i.e., those shown in yellow in Fig. 10) would be expected to increase fledgling production on those territories.

Fort Jackson

Regression tree analysis for Fort Jackson indicated that territories having greater than 14.3% mean herbaceous groundcover had the largest groups, and there were 11 such territories (Fig. 11). Further analyses revealed that alternative thresholds occurred at 162.9 stems/ha (65.9 stems/ac) and 2.63 m^2/ha (11.5 ft^2/ac) basal area of pines 10.2-25.4 cm (4-10 in) dbh (Table 4). In other words, if herbaceous groundcover was excluded from the analysis, the next-best regression tree splits identified territories containing less than 162.9 stems/ha (65.9 stems/ac) or less than 2.63 m^2/ha (11.5 ft^2/ac) basal area of small pines as having larger groups.

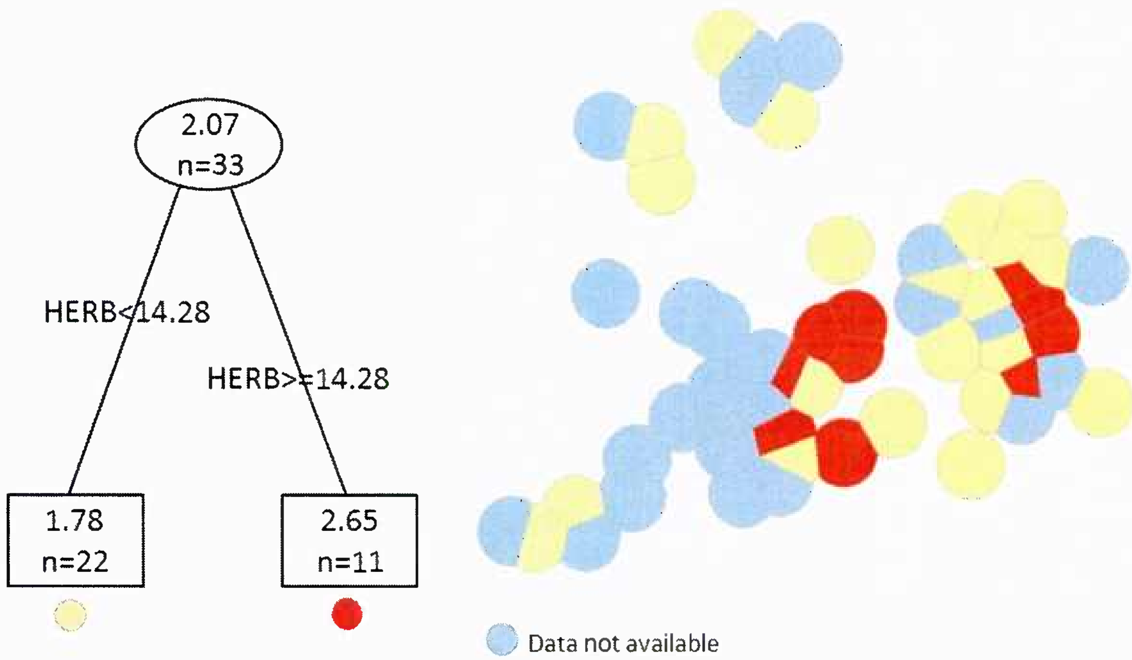

Figure 11. Left panel shows a pruned regression tree for evaluating the relationship between group size and 14 habitat metrics at Fort Jackson, SC. Each node is labeled with the mean group size (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Jackson with higher (red) and lower (yellow) group size as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from additional herbaceous groundcover (> 14.28%),

The most influential habitat feature associated with fledgling production at Fort Jackson was also herbaceous groundcover (Fig. 12). The same 11 territories with greater than 14.28% mean herbaceous groundcover produced more fledglings (mean of 1.47 fledglings) than those with less than 14.28% mean herbaceous groundcover (mean of 0.733 fledglings; Fig. 12). Of the 22 territories with less than 14.28% herbaceous groundcover, those that also contained more than 162.9 stems/ha (65.9 stems/ac) of pines 10.2-25.4 cm (4-10 in) dbh had the lowest overall fledging production (mean of 0.386 fledglings). Alternative thresholds for fledgling production occurred at similar values of small pines as did alternative thresholds for group size (162.9 stems/ha [65.9 stems/ac] or less than 2.65 m^2/ha [11.5 ft^2/ac] basal area; Table 4).

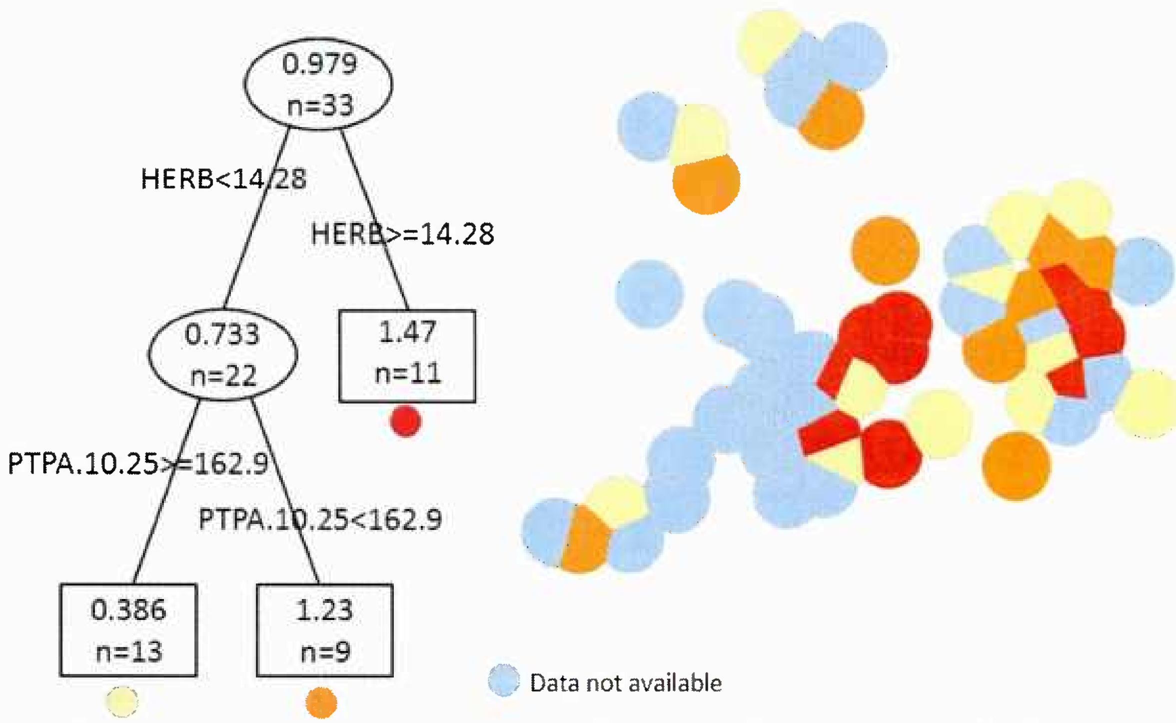

Figure 12. Left panel shows a pruned regression tree for evaluating the relationship between fledgling production and 14 habitat metrics at Fort Jackson, SC. Each node is labeled with the mean fledgling production (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Jackson with higher (red), intermediate (orange), and lower (yellow) fledgling production as determined by the regression tree splits. Together, these results indicate that territories shown in orange might benefit from additional herbaceous groundcover (> 14.28%), whereas those shown in yellow might benefit from additional herbaceous groundcover (>14.28%) and reduced PTPA.10.25 (< 162.9 stems/ha or 65.9 stems/ac).

The results of regression tree analysis for group size and fledgling production at Fort Jackson were very concordant. The importance of higher herbaceous groundcover and lower numbers and basal area of small pines was revealed in both analyses (Figs 11 and 12, Table 4). Indeed, the same 11 territories with > 14.28% mean herbaceous groundcover experienced the largest group sizes and highest fledgling production, and alternative and secondary splits were identified at the same density (162.9 stems/ha or 65.9 stems/ac) of small pines. Increasing herbaceous groundcover to greater than 14% would be expected to increase group size and fledging production, on the yellow and orange territories shown in Figures 11 and 12. A possible reason for the prominence of small pines in our models is the relatively high basal area and number of pine stems of pines 10.2-25.4 cm (4-10 in) dbh at Fort Jackson compared to the other sites (Fig. 4d, e). This is especially true for the territories shown in yellow in Figure 12. Note that the threshold values, like the average values for Fort Jackson, are low for groundcover and high for small pines and hardwoods. Our analysis thus suggests that the small group sizes (Fig. 2) and relatively low fledgling productivity (Fig. 3) at Fort Jackson may be attributable to an overly dense midstory consisting of both pines and hardwoods and resulting suppression of herbaceous groundcover (Hiers et al. 2007). Hence management should be directed toward midstory reduction.

Fort Benning

Regression tree analysis for Fort Benning highlighted the importance of large pines and herbaceous groundcover for enhancing mean territory group size. Larger groups (mean of 2.7 adults) occurred on territories with more than 44.7 pine stems/ha (18.1 stems/ac) of pines > 35 cm (14 in) dbh, in comparison to territories with less than 44.7 pine stems/ha (18.1 stems/ac) (mean of 2.4 adults; Fig. 13). However, of 224 territories with PTPA.35 < 44.7 pine stems/ha (18.1 stems/ac), those that had mean herbaceous groundcover of more than 27.2% had relatively larger groups (mean of 2.6 adults) that those with herbaceous groundcover of less than 27.2% (mean of 2.3 adults). Thus, it seems that the negative effects on group size of having fewer large pines can be partly overcome if herbaceous groundcover is sufficient. These results are reiterated in Table 4, which shows alternative splits (i.e., if PTPA.35 was excluded from the analysis) at greater than 5.5 m^2/ha (23.9 ft^2/ac) mean pine basal area of pines > 35 cm (14 in) dbh or more than 27.4% mean herbaceous groundcover.

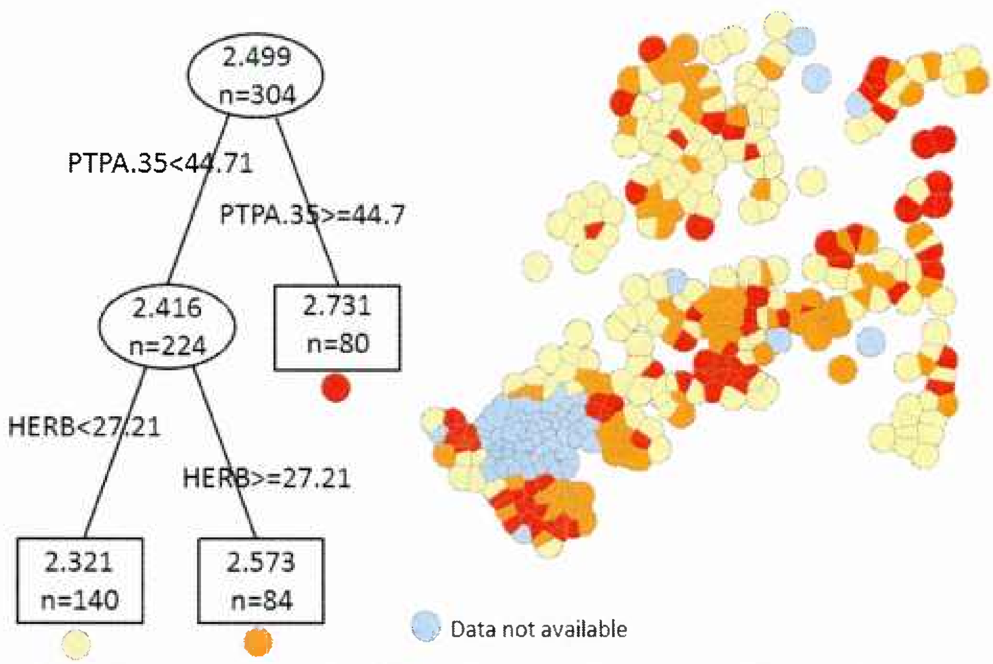

Figure 13. Left panel shows a pruned regression tree for evaluating the relationship between group size and 14 habitat metrics at Fort Benning, GA. Each node is labeled with the mean group size (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Benning with higher (red), intermediate (orange) and lower (yellow) group size as determined by the regression tree splits. Together, these results indicate that territories shown in orange might benefit from additional PTPA.35 (> 44.7 stems/ha or 18.1 stems/ac), whereas those shown in yellow might benefit from additional PTPA.35 (> 44.7 stems/ha or 18.1 stems/ac) and additional herbaceous groundcover (> 27.21%).

Large pines were also strongly associated with fledgling production at Fort Benning (Fig. 14). There was a threshold in the number of pine stems/ha of pines > 35 cm (14 in) dbh whereby territories with more than 24.2 stems/ha (9.8 stems/ac) produced more fledglings (mean of 1.5) when compared to those with fewer than 24.2 stems/ha (9.8 stems/ac) (mean of 0.5; Fig. 14).

Further analyses revealed that alternative thresholds occurred at 3.1 m^2/ha (13.5 ft^2/ac) basal area of pines > 35 cm dbh and 1.6 m^2/ha (7 ft^2/ac) basal area of pines 10.2-25.4 cm (4-10 in) dbh (Table 4). In other words, if PTPA.35 was excluded from the analysis, the next-best regression tree splits identified territories containing greater than 3.1 m^2/ha (13.5 ft^2/ac) basal area of large pines or less than 1.6 m^2/ha (7 ft^2/ac) basal area of small pines.

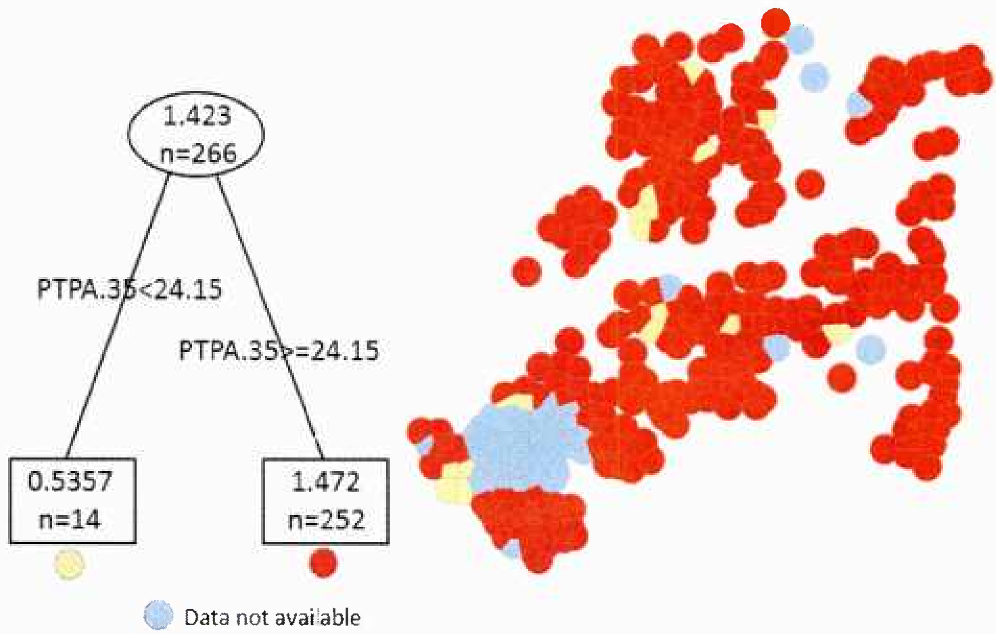

Figure 14. Left panel shows a pruned regression tree for evaluating the relationship between fledgling production and 14 habitat metrics at Fort Benning, GA. Each node is labeled with the mean fledgling production (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Benning with higher (red) and lower (yellow) fledgling production as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from additional PTPA.35 (> 24.15 stems/ha or 9.8 stems/ac).

When comparing the requirements for group size versus fledgling production at Fort Benning, group size appeared more dependent on large numbers and high basal area of large pines; that is, the thresholds for PBA.35 and PTPA.35 were higher for group size than they were for fledgling production (Table 4). This pattern is reinforced by the finding that the largest groups occurred when at least 37% of a territory met the threshold of 44.7 stems/ha (18.1 stems/ac) of pines > 35 cm (14 in) dbh, whereas only 12.5% of a territory needed to meet the threshold of 24.2 stems/ha (9.8 stems/ac) in order for fledgling production to be maximized. Thus, it may be most helpful for Fort Benning to focus on territory quality as it relates to group size (Fig. 13). Since increasing the number of large pines is not feasible in the short term, improving ground cover condition on territories with the smallest groups (i.e., those shown in yellow in Fig. 13) might be the most effective means to enhance foraging habitat conditions. Note that Fort Benning, along with Fort Jackson, had the smallest numbers of large pines among the sites examined (Table 4).

Fort Stewart

Results of regression tree analysis for group size at Fort Stewart at first seem to contradict the accepted understanding of RCW habitat quality (Fig. 15). Specifically, 51 territories with more than 9.2 m^2/ha (39.9 ft^2/ac) basal area of pines > 35 cm (14 in) dbh had lower group sizes (mean of 2.1 adults) than 296 territories with less than 9.2 m^2/ha (39.9 ft^2/ac) basal area of pines > 35 cm (14 in) dbh (mean of 2.3 adults). This is in contrast to the many studies showing positive effects of large pines, but group size and productivity can also decrease with high density of large pines (Hardesty et al. 1997; James et al. 1997; Walters et al. 2002), and the threshold value is twice the recommended minimum density of large pines (Table 2). The second split in the regression tree (Fig. 15) reveals that the lowest overall group sizes occurred on territories that had a combination of less than 9.2 m^2/ha (39.9 ft^2/ac) basal area of pines > 35 cm (14 in) dbh and less than 0.42 m^2/ha (1.8 ft^2/ac) basal area of pines 10.2-25.4 cm (4-10 in) dbh (mean of 1.8 adults). Thus, territories with a combination of lower pine basal area of large pines (PBA.35 < 9.2 m^2/ha or 39.9 ft^2/ac) and higher pine basal area of small pines (PBA.10.25 >= 0.42 m^2/ha or 1.8 ft^2/ac) maintain the largest RCW groups. These results indicate that the present densities of small pines at Fort Stewart, which are relatively low (Fig. 4d), do not have a negative impact on foraging habitat quality.

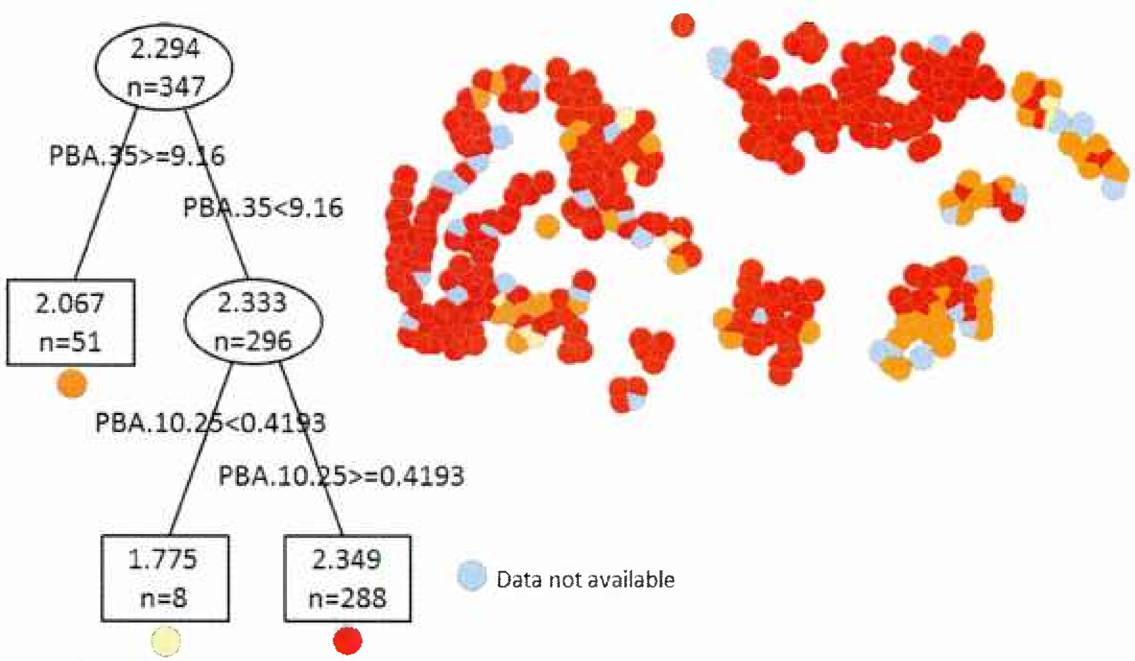

Figure 15. Left panel shows a pruned regression tree for evaluating the relationship between group size and 14 habitat metrics at Fort Stewart, GA. Each node is labeled with the mean group size (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Stewart with higher (red), intermediate (orange), and lower (yellow) group size as determined by the regression tree splits. Together, these results indicate that territories shown in orange might benefit from reduced PBA.35 (< 9.16 m^2/ha or 39.9 ft^2/ac), whereas those shown in yellow might benefit from additional PBA.10.25 (> 0.4193 m^2/ha or 1.8 ft^2/ac).

The most influential habitat feature associated with fledgling production at Fort Stewart was herbaceous groundcover (Fig. 16). Territories with greater than 14% mean herbaceous groundcover produced more fledglings (mean of 0.95) than those with less than 14% mean herbaceous groundcover (mean of 0.7; Fig. 16). The highest fledging production overall (mean of 1.16) occurred on 44 territories that had a combination of herbaceous groundcover greater than 14% and more than 8.2 m^2/ha (35.9 ft^2/ac) basal area of pines > 35 cm (14 in) dbh. Thus, although the importance of higher basal area of large pines for group size was somewhat ambiguous (see above), it is evidently still associated with greater fledging production at Fort Stewart. Further analyses revealed that alternative thresholds occurred at 6.7 m^2/ha (29.3 ft^2/ac) basal area and 93.5 pine stems/ha (37.9 stems/ac) of pines of pines 25.4-35 cm (10-14 in) dbh (Table 4). In other words, if herbaceous groundcover was excluded from the analysis, the next-best regression tree splits identified territories containing greater than 6.7 m^2/ha (29.3 ft^2/ac) basal area or more than 93.5 pine stems/ha (37.9 stems/ac) of medium pines.

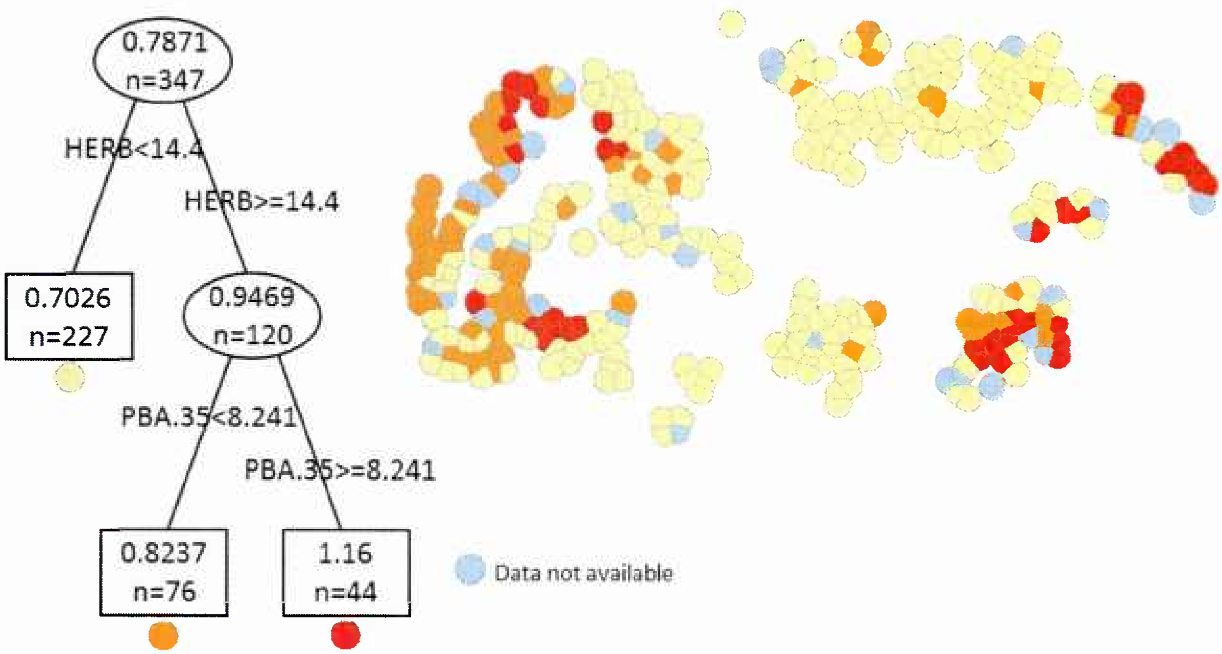

Figure 16. Left panel shows a pruned regression tree for evaluating the relationship between fledgling production and 14 habitat metrics at Fort Stewart, GA. Each node is labeled with the mean fledgling production (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Stewart with higher (red), intermediate (orange), and lower (yellow) fledgling production as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from additional herbaceous groundcover (> 14.4%), whereas those shown in orange might benefit from additional PBA.35 (> 8.241 m^2/ha or 35.9 ft^2/ac).

Basal area of large pines was clearly influential for both group size and fledgling production at Fort Stewart. Group size analysis also revealed that the presence of higher basal area (> 0.42 m^2/ha or 1.8 ft^2/ac) of small pines is preferable when basal area of large pines is lower (< 9.2 m^2/ha or 39.9 ft^2/ac). Finally, improving ground cover condition (greater than 14% for more than 19.5% of a territory, Table 4) would be expected to improve fledgling production on territories shown in yellow in Figure 16. Our results for Fort Stewart contain some enigmatic components. The negative effect of large pines on group size contradicts results elsewhere, although the high threshold value for this effect may indicate the existence of some overstocked stands of large trees. If an overly dense canopy is indeed the source of this effect, these territories could readily be improved by thinning. A possible positive effect of medium pines on fledgling production is also contrary to some previous studies that suggested negative impacts of medium pines at high densities (Walters et al. 2002), and in this case the threshold value is high. In contrast, positive effects of herbaceous groundcover and of large trees (at a lower threshold value) on fledgling productivity are in accordance with results from other installations.

Fort Polk

The two RCW populations at Fort Polk differed non-significantly in mean group size (Polk: 2.52 ± 0.1 adults, Peason Ridge: 2.32 ± 0.14 adults; $t_{104} = -1.19$, $p = 0.236$) and significantly in fledgling production (Polk: 0.96 ± 0.07 fledglings, Peason Ridge: 0.7 ± 0.11 fledglings; $t_{104} = -2.04$, $p = 0.044$). However, regression tree analyses indicated that higher group sizes and fledgling production nonetheless occurred on certain territories with particular habitat features at Peason Ridge. Furthermore, including population as a factor in the following analyses did not change results. In other words, differences among the habitat features of territories were more indicative of higher- and lower-quality territories than were differences between the two populations.

Regression tree analysis for Fort Polk indicated that group size was associated with the number and basal area of pines of different size classes; however results were somewhat difficult to interpret. The largest groups occurred on territories that had a combination of less than 2 m^2/ha (8.7 ft^2/ac) pine basal area of pines 10.2-25.4 cm (4-10 in) dbh, less than 9.3 m^2/ha (40.3 ft^2/ac) pine basal area of pines > 35 cm (14 in), and more than 37.8 stems/ha (15.3 stems/ac) of pines 25.4-35 cm (10-14 in) dbh (mean of 3.5 adults; Fig. 17). In other words, territories with more medium-sized pines, but fewer small and large-sized pines (dark red in Figure 17), appeared to have the best conditions for maintaining larger groups. Combined with the results from Fort Stewart this suggests that very high densities of large pines can be detrimental, contrasting with the positive benefits of open stands of large pines, as others have noted (Hardesty et al. 1997; James et al. 1997, 2001; Walters et al. 2002). These interactions among numbers and density of pines of different size classes may reflect variation in pine canopy and pine midstory densities that impact group size. In any case, the most important habitat feature for group size identified by the regression tree analysis, i.e., the primary split, was basal area of small pines, and interpretations regarding further splits are less reliable (De'Ath and Fabricius 2000).

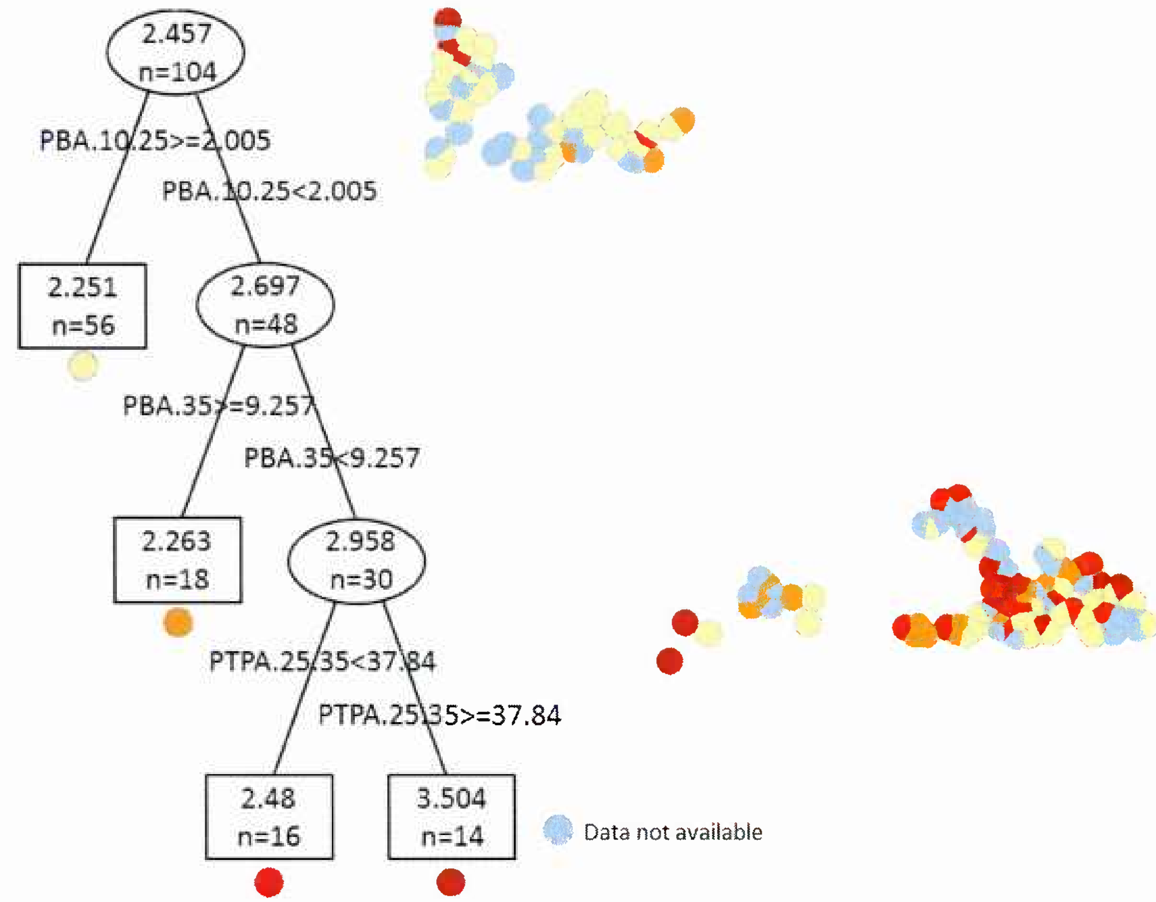

Figure 17. Left panel shows a pruned regression tree for evaluating the relationship between group size and 14 habitat metrics at Fort Polk, LA. Each node is labeled with the mean group size (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Polk with higher (dark red), intermediate (red and orange), and lower (yellow) group size as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from reduced PBA.10.25 (< 2.005 m^2/ha or 8.7 ft^2/ac), whereas those shown in orange might benefit from reduced PBA.35 (< 9.257m^2/ha or 40.3 ft^2/ac), and those shown in red might benefit from additional PTPA.25.35 (> 37.84 stems/ha or 15.3 stems/ac).

The most influential habitat feature associated with fledgling production at Fort Polk was also PTPA.10.25. Territories with fewer than 111.1 mean pine stems/ha (45 stems/ac) of pines 10.2-25.4 cm (4-10 in) dbh produced more fledglings (mean of 1.1) than those with more than 111.1 mean pine stems/ha (45 stems/ac) of pines 10.2-25.4 cm (4-10 in) dbh (mean of 0.64; Fig. 18). Interestingly, examination of alternative thresholds for group size and fledgling production showed that the two were quite concordant with respect to thresholds of small pines (Table 4). Specifically, the thresholds identified in the models for group size (PBA.10.25 < 2 m^2/ha or 8.7 ft^2/ac and PTPA.10.25 < 95.9 stems/ha or 38.8 stems/ac) were very close to the values identified for fledgling production (PBA.10.25 < 2.3 m^2/ha or 9.8 ft^2/ac and PTPA.10.25 < 111.1 stems/ha or 45 stems/ac). Note that the basal area threshold is very similar to that in the Recovery Plan (USFWS 2003) while the stem number threshold is much higher than the Recovery Plan value.

On the other hand, an alternative threshold was identified for number of hardwood stems/ha in the 10.2-25.4 cm (4-10 in) dbh class that was inconsistent between the two, with greater HTPA.10.25 preferred for group size, but lower HTPA.10.25 preferred for fledgling production (Table 4). Again, these results should be interpreted with caution as alternative thresholds are identified only after exclusion of the top variables from the initial regression tree models.

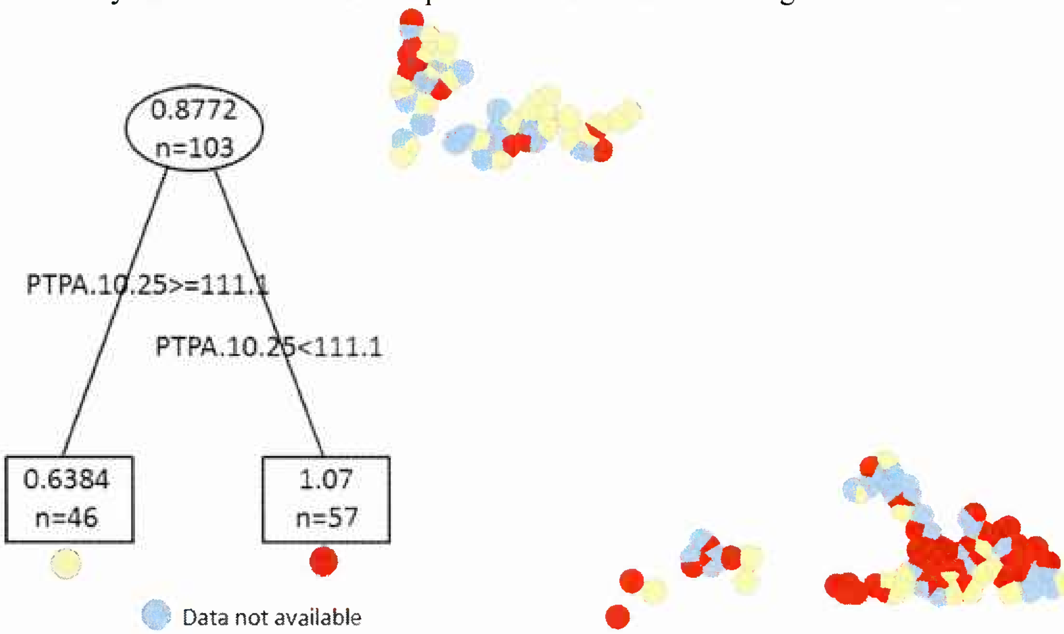

Figure 18. Left panel shows a pruned regression tree for evaluating the relationship between fledgling production and 14 habitat metrics at Fort Polk, LA. Each node is labeled with the mean fledgling production (above) and number of territories (below) falling into that category. Each branch is labeled with the habitat metric and its threshold value associated with that split. Internal nodes are represented by ellipses and terminal nodes are represented by rectangles. Right panel shows the territories at Fort Polk with higher (red) and lower (yellow) fledgling production as determined by the regression tree splits. Together, these results indicate that territories shown in yellow might benefit from reduced PTPA.10.25 (< 111.1 stems/ha or 45 stems/ac).

Small pines were the key habitat metrics identified in regression tree analyses for both group size and fledgling production. Fewer small pines/ha and lower basal area of small pines were preferable in both cases. Further, the thresholds of less than 2 m^2/ha (8.7 ft^2/ac) pine basal area of pines 10.2-25.4 cm (4-10 in) dbh (for group size), and fewer than 111.1 mean pine stems/ha (45 stems/ac) of pines 10.2-25.4 cm (4-10 in) dbh (fledgling production), were most beneficial if occurring on 25.4% and 32% of a territory, respectively.

1.5 DISCUSSION

The value of foraging habitat for the red-cockaded woodpecker has received much attention through extensive research on resource selection, habitat use, and associations between habitat features and RCW fitness (reviewed in Walters et al. 2002). Red-cockaded woodpeckers are known to select older and larger pine trees for foraging, and they tend to forage in habitat patches containing a greater density of older and larger pines, a less prominent hardwood midstory, and a lower density of medium and small pines (Hardesty et al. 1997; Doster and James 1998; Walters et al. 2002). Accordingly, larger woodpecker groups and higher reproductive success have been associated with greater herbaceous groundcover, greater density of older and larger pines, a less prominent hardwood midstory, and a lower density of small and medium pines (Hardesty et al. 1997; James et al. 1997, 2001; Walters et al. 2002; Butler and Tappe 2008). Finally, group size and reproduction can be negatively affected by a high density of large pines (Hardesty et al. 1997; James et al. 1997; Walters et al. 2002). Results from our range-wide summary of the conditions used by RCWs and our regression tree analyses generally supported these findings. Greater percentage of herbaceous groundcover and fewer pine stems or lower basal area of small pines were associated with group size and/or fledgling production at four of five sites (Fort Bragg, Fort Jackson, Fort Benning, and Fort Stewart; Table 4). Density of pine stems and basal area of large pines (> 35 cm [14 in] dbh) also emerged as key habitat metrics for group size and/or fledgling production at four sites (Fort Bragg, Fort Benning, Fort Stewart, and Fort Polk). However, our findings also highlighted localized thresholds and ranges of foraging habitat conditions that are not fully captured in the current foraging habitat guidelines (USFWS 2003).

Across all 10 sites, mean group size was 2.45 (1.9-2.96) adults, and mean fledgling production was 1.27 (0.77-1.79) fledglings per territory per year. Fledgling production was generally higher in northern and inland populations when compared to southern and coastal populations, but neither fledgling production nor group size showed significant associations with latitude or longitude (Figs 2 and 3). Analyses of foraging habitat at a subset of five sites with comparable habitat data showed that available territories (i.e., those that were occupied by at least one adult over a 5-year period) displayed a range of foraging habitat metric values (Table 3). Ranges of foraging habitat metrics on the 25% most productive territories were similar to those on the least productive territories and on all territories combined for most habitat metrics at most sites (Table 3). One notable exception was the higher mean percent herbaceous groundcover that was present on the most productive territories at all sites, whereas the mean values for the least productive territories were lower. Differences among sites contributed to the variation in foraging habitat metrics (Figs. 4 and 5). In particular, herbaceous groundcover (Fig. 4g) and presence and density of hardwoods (Fig. 4h, Fig. 5b-g) were quite variable, with the two inland north-eastern sites (Fort Bragg and Fort Jackson) exhibiting elevated hardwood components when compared to other sites, especially among smaller stem size classes. Many territories fell outside of the bounds of Recovery Plan guidelines for good quality habitat, though this depended on the particular habitat metric in question. Most territories were below the recommended maximum of 9.2 m^2/ha (40 ft^2/ac) basal area for medium-sized pines (25.4-35 cm [10-14 in] dbh; Fig. 4c) and above the recommended 4.6 m^2/ha (20 ft^2/ac) basal area for large-sized pines (> 35 cm [14 in] dbh class; Fig. 4b), few territories were below the recommended maximum of 2.3 m^2/ha (10 ft^2/ac) basal area and 50 stems/ha (20 stems/ac) for small-sized pines (10.2-25.4 cm [4-10 in] dbh; Fig. 4d, e), and about half of territories met the lower threshold of 40% herbaceous groundcover (Fig. 4g) and hardwood midstory index of less than 3 (Fig. 4h).

Current foraging habitat guidelines and the RCW Foraging Matrix Application were developed primarily from detailed studies at key sites with fire-maintained and restored habitats, including Fort Bragg, NC, and Apalachicola National Forest, FL (James et al. 1997, 2001; Walters et al. 2002). Over the last decade, the use of fire has become widespread and restored habitats differ greatly in attributes such as pine density, hardwood density, and ground cover condition, as discussed above. We found that territory-level evaluation scores from the RCW Matrix Application were generally not strong predictors of group size or fledging production at five military installations (Figs 6 and 7). Similarly, the number of hectares of a territory receiving a high RCW Matrix score (4 or 5) was only significantly associated with RCW fitness in a few instances (Fig. 8), though it should be noted that associations were for the most part positive (i.e., higher scores were generally associated with larger group size or higher fledgling production on a territory).

The lack of a strong association between RCW Matrix scores and fitness is perhaps not completely unexpected. Low territory-level scores can be caused by too few stands within the territory meeting the GQFH requirements, thus lowering the overall territory score even if some of the available stands are close to being GQFH. Indeed, the fact that a stand must meet all requirements set out in the recovery plan in order to be considered GQFH may be overly restrictive. Also, a multitude of factors other than habitat quality are known to contribute to variation in fledging production (and thereby indirectly group size), such as weather, number of helpers, and age of breeders (Lennartz et al. 1987; Walters 1990; Neal et al. 1993), limiting the strength of the correlation between these variables and habitat. Even if foraging habitat was perfectly linked to RCW fitness, breaking down complex and potentially interacting habitat components into a single score is unlikely to directly capture the quality of foraging habitat across the range of the species. Finally, some variables are more closely tied to fitness than others, so combining them with other variables of less importance in a single score likely dilutes fitness correlates. Indeed, we found that certain habitat metrics included in the RCW Matrix Application were identified more often than others as important to fitness in our regression tree analyses (Table 5). Specifically, large pines, small pines, and herbaceous groundcover consistently appeared in regression tree analyses, whereas, large hardwoods were not identified as important (positively or negatively) in any result and, with the exception of Fort Jackson, negative effects of hardwoods were not evident. These results indicate that early foraging habitat guidelines and the RCW Matrix Application have been essential tools for improving RCW foraging habitat quality. As a result, many "thresholds" in foraging habitat metrics were likely crossed, leading to improvements in foraging habitat quality. Thus, the value of our regression tree analyses is that they reveal *current* site-specific thresholds in habitat metrics that might lead to further improvements in habitat quality and bird fitness, over the improvements already obtained by managers.

Table 5. Foraging habitat metrics included in the RCW Foraging Matrix Application and the number of times each metric was identified in regression tree models as a primary, secondary, or alternative split, at all five military installations combined. "+" and "-" indicate whether increases or decreases, respectively, were identified as leading to larger group sizes or higher fledgling production, and "x" indicates that the habitat metric was not identified in any models. For example, PBA.25.35 appeared in only one model and higher values lead to higher fitness, whereas PBA.10.25 appeared in more than four models and higher values lead to higher fitness in some models and lower fitness in others.

		0	1	2	3	>= 4
Large pines	PBA.35					+
	PTPA.35				+	
Medium pines	PBA.25.35		+			
	PTPA.25.35			+		
Small pines	PBA.10.25					+\ -
	PTPA.10.25					+\ -
Large hardwoods	HBA.35	x				
	HTPA.35	x				
Medium hardwoods	HBA.25.35		+			
	HTPA.25.35		+			
Small hardwoods	HBA.10.25	x				
	HTPA.10.25			+\ -		
Hardwood midstory	HWDMID	x				
Herbaceous groundcover	HERB					+

With regard to herbaceous groundcover, we found that thresholds in percentage herbaceous groundcover relating to higher group size and/or fledgling production ranged among sites from 14% to 59%. Threshold values tended to mirror mean herbaceous groundcover values at each site, with higher thresholds at sites having higher mean herbaceous values (Table 4). The one site for which herbaceous groundcover was not identified as being among the most important habitat metrics for group size and fledgling production, Fort Polk, was the site with the highest mean value of herbaceous groundcover, with most territories already falling well within the guidelines of the recovery plan (USFWS 2003; Fig. 4g). The 40% ground cover figure presented in the Recovery Plan (USFWS 2003) derives from the work of James et al. (1997, 2001) on Apalachicola National Forest and represents a sixth threshold value. These results clearly indicate that herbaceous groundcover is a critical attribute of foraging habitat quality. One interpretation of differences in threshold values among sites is that there is geographic variation in the range of values over which fitness effects occurred, and thus that different management targets are appropriate for different sites. Another interpretation is that greater herbaceous groundcover provides benefits up to a limit, represented by Fort Polk, above which further increases do not result in increased fitness, and the sites analyzed differ in where they were relative to that upper limit. Almost certainly both explanations apply. At Fort Stewart, for instance, the lower-quality soils of the Southern Coastal Plain might preclude the establishment of a herbaceous layer as rich as that of the Sandhills Ecoregion sites, namely Fort Bragg and Fort Benning, leading to a lower threshold for the association between herbaceous groundcover and fitness at Fort Stewart. However, this interpretation cannot account for the equally low herbaceous component and thresholds at Fort Jackson, which also occurs in the Sandhills Ecoregion. The low ground cover values reported for Fort Jackson may be the effect of suppression by pine and hardwood midstory. Thus, appropriate management has the potential to increase herbaceous groundcover and likely result in a new, higher threshold. Conversely, the large difference between Fort Bragg and Fort Benning cannot be explained in this way and likely reflects geographic variation in the appropriate value for groundcover at least in part. Detailed studies of the variation in plant communities within sites and their response to fire and other management actions could reveal the geographic variation in limits to herbaceous groundcover and result in site-specific management targets. Until then, the threshold values for herbaceous groundcover we identified could serve as localized guidelines for current management at our study sites, and perhaps for other nearby locations.

Second, our results indicate the benefits of more large pines (> 35 cm [14 in] dbh) at several locations. We were able to evaluate the impact of large trees on woodpecker group size and reproduction over a greater range of densities and basal areas than when the Recovery Plan was updated because there are now more large trees on the landscapes. Large pine densities above 50.2 stems/ha (20.3 stems/ac) and 44.7 stems/ha (18.1 stems/ac) were associated with larger RCW groups at Fort Bragg and Fort Benning, respectively. Similarly, large pine basal areas of 7.45 m^2/ha (32.5 ft^2/ac) and 5.48 m^2/ha (23.9 ft^2/ac) were associated with larger groups at the same two sites. These values are equal to or greater than the minimum stem density and basal area for large pines that were recommended in the Recovery Plan (4.6 m^2/ha or 20 ft^2/ac and 45 stems/ha or 18 stems/ac; Table 2). Our results thus reinforce the importance of large pines and even indicate that somewhat higher recommendations might be broadly appropriate. That is, fitness benefits may continue to accrue with large pine densities and basal area that extend above the levels identified in the Recovery Plan. However, there is likely also an upper bound to benefits of large trees. The Recovery Plan does not currently specify a maximum density for large pines, but we identified an upper threshold for basal area (~9.2 m^2/ha or 40 ft^2/ac, Fig. 17 and Table 4) at two sites – Fort Stewart and Fort Polk – above which RCW group sizes were lower. Interestingly, Walters et al. (2002) also identified nearly the same upper limit when they reported that that percentage of patches used by foraging RCWs at Fort Bragg decreased with pine (> 35.6 cm [14 in] dbh) densities of more than 90 stems/ha (36.4 stems/ac) of pines (roughly 9 m^2/ha or 39 ft^2/ac basal area). Thus, 9.2 m^2/ha (40 ft^2/ac) basal area and 90 stems/ha (36.4 stems/ac) may be appropriate upper limits for large pines. Perhaps extremely high stocking rates may provide so much shade as to affect production of ground cover. We did not identify any lower density limit for large trees, below which habitat becomes unacceptable. Of course it also remains critical to retain large old-growth pines within the core habitat area in order to provide future potential nest and roost trees.

Several studies have reported negative effects of high densities of medium-sized pines (25.4-35 [10-14 in] cm dbh) on RCW group size and reproduction (Hardesty et al. 1997; James et al. 1997, 2001; Walters et al. 2002). Medium pines were not identified as being among the most important habitat metrics in many of our regression tree analyses, and interestingly, when medium pines did appear in our models, they showed positive rather than negative effects on group size or reproduction. At Fort Bragg, a secondary regression tree split identified larger RCW groups occurring on territories with more than 50.4 stems/ha (20.4 stems/ac) of medium pines, and at Fort Stewart, thresholds for higher fledgling production were identified at 6.72 m^2/ha (29.3 ft^2/ac) and 93.5 stems/ha (37.9 stems/ac) (Table 4). The Recovery Plan guidelines recommend medium pine stocking rates with a maximum basal area of 9.2 m^2/ha (40 ft^2/ac) and do not specify a maximum number of stems/ha (USFWS 2003). When the analyses leading to the Recovery Plan guidelines were conducted, dense pine stands were commonplace and medium pines may have been associated with over-stocking. Thinning and other forms of management have been used to replace dense stands of the past with open, park-like stands on many landscapes. As a result of this and of maturation of the forests, as noted previously, the vast majority of territories on all sites fell below the recommended maximum for medium pine stocking (Fig. 4c). Medium pine basal area is the metric for which the desired level identified in the Recovery Plan has been most successfully achieved, which may explain both the rarity of medium pines in our regression tree models and the fact that higher basal area or numbers of medium pines were occasionally favored. Positive effects of medium pines were identified at levels far below the recommended maximum in the Recovery Plan. These results indicate that current densities and numbers of medium pines do not negatively affect group size or fledgling production and that the current recommended maximum of 9.2 m^2/ha (40 ft^2/ac) may be appropriate, or that it could be reduced.

Fourth, our regression tree results revealed upper and lower thresholds for small pine (10.2-25.4 cm [4-10 in] dbh) basal area and densities that were associated with higher and lower group size and fledgling production. As noted above, very few sites were below the recommended maximum of 2.3 m^2/ha (10 ft^2/ac) basal area with fewer than 50 stems/ha (20 stems/ac) of small pines (Fig. 4d, e). Thus, it should not be surprising that upper thresholds, around 2 m^2/ha (8.7 ft^2/ac) basal area of small pines, were identified for group size and/or reproduction at three sites (Fort Jackson, Fort Benning, and Fort Polk; Table 4). In contrast, the upper thresholds for number of stems/ha of small pines that emerged from our analyses were markedly higher than the Recovery Plan standard (ranging from ~96-298 stems/ha or 39-120 stems/ac; Table 4). Further, lower thresholds for basal area (>= 0.42 m^2/ha or 1.8 ft^2/ac) and number of stems/ha (>= 17.4 stems/ha or 7 stems/ac) were associated with larger groups at Fort Stewart. Our results thus support the recommended maximum of 2.3 m^2/ha (10 ft^2/ac) basal area for small pines, but further indicate that the maximum of 50 stems/ha (20 stems/ac) could be raised to a higher value. The discrepancy is likely due to the presence of large numbers of very small pine stems on many landscapes. Given that an overly-dense midstory is an issue with small pines, and that regeneration from very small pines is essential to forest health and a desired consequence of restoration of fire regimes, a basal area standard is likely sufficient to achieve desired goals. Our results indicate that overly dense pine midstories continue to persist on many landscapes, and thus that a restrictive small pine metric is needed. Finally, our results also suggest that lower thresholds may exist for small pines, but based on only one site showing this relationship we are not able to produce a robust estimate for minimum small pine basal area or number of stems. It is also possible that the lower threshold may be caused not by the pines but by another factor associated with the absence of small pines, for example absence of fire.

A final notable finding from our regression tree analyses relates to hardwood midstory index and the presence of hardwoods. The negative impact on RCW group size or fledgling production of a tall, dense hardwood midstory was not identified in any regression tree model (Table 5). This result does not necessarily contradict accepted theory regarding the negative effects of a prominent hardwood midstory (Walters et al. 2002) as the lack of hardwood midstory measures in our models may simply indicate that hardwoods were not present in problematic densities and are no longer impacting RCWs. Overall, hardwood stocking rates in three size classes (10.2-25.4 cm [4-10 in], 25.4-35 cm [10-14 in], and > 35 cm [14 in] dbh) were rarely identified in regression tree models (Table 4). One exception occurred at Fort Bragg, where higher basal area (>= 0.46 m^2/ha or 2 ft^2/ac) and greater number of stems/ha (>= 5.23 stems/ha or 2.1 stems/ac) of medium hardwoods were associated with enhanced fledgling production. It is notable that this effect was evident on a landscape in which the hardwood midstory index was above the recommended maximum. A second and somewhat anomalous result at Fort Polk indicated that the presence of more small hardwoods (>= 34.4 stems/ha or 13.9 stems/ac) was associated with larger groups, but the presence of fewer small hardwoods (< 8.44 stems/ha or 3.4 stems/ac) was associated with higher fledgling production. Fort Polk had the lowest hardwood component among the sites, so again, these results could indicate that current numbers and densities of hardwoods at the sites surveyed are not high enough to cause negative effects on RCW group size and productivity. Overall, our results suggest that a modest hardwood component, in contrast to a prominent hardwood midstory (i.e., dense hardwood midstory layer), does not produce negative impacts and may even be beneficial to RCWs. The finding is consistent with recent research indicating that negative effects of a dense hardwood midstory operate through groundcover suppression, that a substantial midstory layer is needed in order to suppress groundcover, and that past correlations between hardwood midstory and RCWs were difficult to separate from effects of suppressed fires (Hiers et al. 2007). Accumulation of leaf litter in the absence of fire, rather than midstory shading, appears to have a greater effect on reducing understory diversity (Provencher et al. 2001; Hiers et al. 2007). The current recommended maximum hardwood midstory index thus may be too low, and it might be better to manage for a variable target that could result in some values approaching the index value, rather than managing for more uniform values well below the target. In other words, managing for an herbaceous groundcover target rather than managing directly for a hardwood midstory target may be beneficial.

Our regression tree results were not changed by the inclusion of territory area as an additional variable, indicating that the foraging habitat metrics identified in our models were more tightly linked to fitness than was territory area. The link between foraging habitat metrics and RCW fitness was also evidenced by the fact that many small territories were among those with the largest groups and highest fledgling production (i.e., small red territories in Figs 9-18). Similarly, Walters et al. (2002) found no relationship between group size and home range size. These authors argued that the area required by RCW groups likely decreases as a function of habitat quality, and the area of high-quality foraging habitat within the home range is thus more important than total home range area. Our results indicated that territory partitions as small as 20 ha could be among the most productive, as long as specific thresholds dictated by the regression trees were met. However, these results assume accurate partitioning and exclusive use of territory partitions by resident RCW groups which is unlikely to be the case for very small territories. Thus further elucidation of the potential effects of territory size, and of high and low density RCW populations, requires further research aimed at testing these assumptions.

The beneficial habitat conditions identified by our results can be linked to prescribed burning. In particular, a rich herbaceous layer, intermediate pine density, and limited hardwood midstory are associated with frequent growing season fire (Outcalt 2006). As noted above, managing for a rich herbaceous layer via prescribed burning (Outcalt and Brockway 2010), rather than managing directly for reduced hardwood midstory, may be broadly appropriate at restored sites.

Our results must be considered in light of several key issues. First, a caveat to our regression tree analyses is that recommendations are predominantly site and territory-specific. The contribution of a specific habitat metric to overall foraging habitat quality will likely depend on local habitat structure and composition, as highlighted by the above discussions of herbaceous groundcover and hardwood midstory. Another related issue is that our analyses revealed natural break-points in relative differences in group size and reproduction *within* sites. Differences in factors such as population growth rate and availability/provision of recruitment sites will clearly influence fitness, weakening habitat-fitness associations and making direct comparisons among sites challenging. Future studies could incorporate these variables, as well as additional factors such as the presence of suitable cavity trees and breeder age and experience. Second, regression trees and thresholds rest on top of existing habitat conditions and are reflective of opportunities for current improvements *in addition* to those achieved in the preceding decades. Habitat restoration efforts such as prescribed burning and hardwood management likely improved habitats substantially, and thereby resulted in the elimination of previous habitat challenges and the crossing of previous thresholds. Similarly, future changes in habitat structure may eliminate the issues identified herein, and thus subsequent regression tree analyses might identify other yet-to-be-defined thresholds and opportunities for improvement in RCW fitness. Thus, we recommend regular revisions and updates to foraging habitat guidelines. One approach would be to apply regression tree analyses similar to ours once every five years, using mean fitness values over the preceding five years and updated forest inventory data. Third, our analyses aimed to identify optimal habitat conditions at each site, but these conditions presumably occurred within a range of acceptable conditions. Identifying the lower limits of what is acceptable was not possible with our dataset for several reasons. Unacceptable habitat would likely be characterized by RCW groups avoiding it entirely, dispersing, or dying, and unoccupied areas would consequently not be managed for woodpeckers. These areas were likely not well-represented in our dataset as they would not be reported in annual breeding surveys. Further, suitable sites that were initially unoccupied may have become occupied in later years following the creation of cavity trees. Indeed, preliminary analyses showed no differences in habitat metrics for sites occupied for the entire 5-year period versus those occupied in only some years, and so we chose to analyze mean group sizes and fledgling production strictly during occupied years so as to remove this potential bias. Future studies should use telemetry to track the resources that are used and those that are avoided by woodpeckers, ideally at multiple sites of varying habitat structure, in order to identify unacceptable habitat conditions.

1.6 CONCLUSIONS

This study provides the first comprehensive analysis of RCW fitness, associated habitat, and foraging habitat quality across the species' range. The results of this study lend support to the 2003 USFWS RCW Recovery Plan by showing associations between RCW fitness and foraging habitat features included in the Plan's guidelines. At the same time, we identify areas where the guidelines could potentially be made more inclusive by highlighting site-specific variation in habitat components important to RCW fitness, and habitat components for which metrics might be altered. All of the latter emerge out of differences between the past landscapes upon which the Recovery Plan standards are based and current landscapes considerably transformed by habitat management, particularly the return of fire, which allowed us to analyze a different, wider range of habitat variation. As habitat restoration and RCW translocation efforts continue, we will no doubt see further increases in variation in the types and quality of habitats that can be occupied by this species.

PART 2: SPACE USE AND RESOURCE SELECTION AT EGLIN AIR FORCE BASE

2.1 INTRODUCTION

Great gains have been made with recent studies of movement, an essential component of survival and reproduction in most organisms. Although trade-offs between tracking equipment size and performance continue to limit the amount and type of data that are available for smaller animals (Wikelski et al. 2007; Nathan et al. 2008; Bridge et al. 2011), recent technological advances have allowed researchers to collect movement data on smaller animals and at finer spatiotemporal scales. These improved techniques have been complimented by the development of a contemporary movement ecology framework that has paved the way for quantitative assessment of the causes, consequences, and mechanistic basis of organismal movement (Nathan et al. 2008). Many studies focused on movement patterns of larger and wide-ranging animals with the help of radio telemetry or global positioning systems (GPS) satellite telemetry (Bergman et al. 2000; Austin et al. 2004; Fryxell et al. 2008; Avgar et al. 2013), but less work has been devoted to studying high-resolution foraging movements of smaller animals and non-migratory territorial residents. Territorial resident species are especially appropriate for studies of fine-scale movement patterns and resource use due to the potential for observing resource limitation and social determinants of movement within their restricted home ranges (Newton 1998). Further, such species may be constrained in space to a central location (e.g., a nest or roost site), and thus may display differential resource selection depending on location within the home range.

The red-cockaded woodpecker (*Picoides borealis*; RCW) is a small resident bird species which has garnered substantial conservation interest because of its status of being endangered with extinction (U.S. Code Title 16, Chapter 35, Section 1531-1544). Previous studies of resource use demonstrated that RCWs selected older, larger pine trees for foraging, and tended to forage in forest patches with greater densities of older and larger pines, less prominent hardwood midstories, and lower densities of medium and small pines (Hardesty et al. 1997; Doster and James 1998; Walters et al. 2002). Red-cockaded woodpeckers occupy large home ranges as conspecific cooperative groups, within which birds make extensive foraging movements (Conner et al. 2001).

Over the past several decades, much RCW habitat has been restored via prescribed burning, hardwood removal, and pine thinning (Conner et al. 2001). Most movement and habitat use results for RCWs were reported primarily from studies prior to the second revision of the RCW Recovery Plan (USFWS 2003). However, restored habitats vary considerably in forest structure and composition (see Part 1), and there is a need to understand how habitat selection is associated with foraging guidelines on these diverse restored habitats. In addition, few studies have documented RCW resource selection within the Southern Coastal Plain Ecoregion (but see Hardesty et al. 1997). A robust population of RCWs inhabits Eglin Air Force Base (AFB), Florida, which is set within the Southern Coastal Plain and characterized by more southern climates, marine-derived sediments, and generally flatter landscapes in comparison to the other ecoregions inhabited by RCWs (Peet 2006). Forests within the Southern Coastal Plain are accordingly different from those in other regions – soils are less productive and large longleaf pines (> 35 cm [14 in] dbh) are rare. For these reasons, movements and habitat use by RCWs may also differ among ecoregions.

We here describe a study of fine-scale space use and resource selection in the RCW in the Southern Coastal Plain site at Eglin AFB. Observers tracked foraging woodpecker groups with GPS, which resulted in substantial high-resolution movement information. Our analyses involved two steps. First, we described within home range movements of RCW groups, with particular emphasis on their use of the territory partitions that are developed to represent foraging areas and that are employed in habitat management (USFWS 2003). Second, we examined patterns of RCW resource selection by comparing the habitat features used by foraging birds with a random selection of un-used resources from within the home range. We evaluated the use of stands according to their habitat features and RCW Matrix Application scores, as well as the use of habitat patches according to their habitat quality scores from the Eglin Foraging Model (described below). We further examined whether the strength of resource selection was influenced by group size or location within the home range, as RCWs are cooperative breeders and central-place foragers (Rosenberg and McKelvey 1999).

2.2 METHODS

Field methods

Observation sessions ($n = 451$), or the set of location points for a given RCW group on a given day, were recorded on 97 territories at Eglin AFB. Observations were recorded during all months, except December, between late February, 2007, and early November, 2008. The majority (77%) of sessions were recorded during the pre-breeding period (March and April; $n = 109$), fledgling-rearing period (June and early July; $n = 114$), and the post-breeding period (September and October; $n = 122$).

During each session, birds were followed by observers outfitted with a global positioning system (GPS; Garmin Legend, Garmin Ltd., Olathe, KS), set to automatically record the geographic coordinates of its location once each minute. Observers arrived at cluster centers at or before sunrise. After RCWs emerged from roost cavities, they foraged together as a group, generally moving away from the territory center. Observers visually observed and recorded the number of birds in each group, and the combination of colored leg bands on birds that had been previously marked. Observers attempted to remain with each RCW group for approximately 1 hr (February 2007 to July 2007) or 2 hr (September 2007 to November 2008) while birds foraged and moved throughout territories. These foraging sessions generally lasted for the duration of the observation session. During the observation sessions, woodpeckers moved from tree to tree, and although individuals were not always on the same tree at the same time, birds remained in the same general areas and regularly made contact calls. Observers followed RCW groups without difficulty, and they attempted to remain within 30 m of at least one group member. Locations recorded within 50 m of the territory center, as defined by the geographic mean of coordinates for cluster trees (see below), were removed to reduce the influence of the pre-foraging social interactions that occurred at sunrise. Observations were also excluded if GPS units failed to estimate a location. Observation sessions were occasionally truncated when birds made sudden long distance movements and observers could not follow them, or when inclement weather prevented the visual observations of foraging birds. Data from nine sessions were removed because they included < 15 observations. In total, 37,109 locations were recorded during the 451 observation sessions.

Habitat metrics and habitat quality models

Standardized forest inventory data were provided by Eglin AFB in the form of forest stand geodatabases (spatial and quantitative stand representations). Habitat metrics included stand age, number of pine stems/ha in three different size classes (10.2-25.4 cm [4-10 in] diameter at breast height [dbh], 25.4-35 cm [10-14 in] dbh, and > 35 cm [14 in] dbh) and an index of hardwood midstory that ranged from 1 to 9 (1 = Low, Sparse; 2 = Low, Moderate; 3 = Low, Dense; 4 = Medium, Sparse; 5 = Tall, Sparse; 6 = Medium, Moderate; 7 = Tall, Moderate; 8 = Medium, Dense; 9 = Tall, Dense). We used these metrics to compute stand-level habitat quality scores with the RCW Foraging Matrix Application (Intergraph Corporation, Huntsville, AL) in ArcMap version 10.0 (Environmental Systems Research Institute [ESRI], Inc., Redlands, CA). Note that fire history and the percentage of herbaceous groundcover can also be included in the RCW Matrix Application's evaluation of foraging habitat quality. As these metrics were not available for Eglin AFB, we re-weighted the available metrics accordingly. For more information on the RCW Foraging Matrix Application, see http://www.fws.gov/rcwrecovery/matrix.html.

Whereas most of the military installations hosting recovery populations of RCWs use the RCW Foraging Matrix Application, Eglin AFB used a separate tool to evaluate foraging habitat quality. The Eglin Foraging Model divides the landscape into habitat patches of 1 ha (2.5 ac) and uses remote sensing from the Thematic Mapper satellite imagery to assign each patch a score from 0 to 3: Unsuitable – cleared (0, non-forested); Unsuitable – forested (1, longleaf pine basal area < 1.2 m^2/ha [5 ft^2/ac]); Suitable – marginal (2, longleaf pine basal area 1.2-5.7 m^2/ha [5-25 ft^2/ac] with a mean of 3.4 [15]); and Suitable – optimal (3, longleaf pine basal area 4.6-18.4 m^2/ha [20-80 ft^2/ac] with a mean of 7.6 [33]). Ground-truthing at monitoring plots supported the ability of remote sensing to designate these categories. Eglin AFB provided us with Eglin Model scores in the form of a geodatabase that covered the study site.

Space use analysis

We defined RCW territory centers at Eglin AFB as the arithmetic mean of the geographic coordinates of roosting and nesting cavity trees, and we used ArcMap version 10.0 to calculate the maximum distance traveled from the territory center by a group during each observation session. We used linear regression to examine the relationship between maximum distance and duration of observation session, and, after controlling for effects of duration of observation session, we used one-way mixed effects ANOVA with territory ID as a random effect to assess whether maximum distance varied with season.

We next evaluated the utility of the territory partitions used by managers to represent the areas available to each group of RCWs. In accordance with the guidelines of the USFWS Recovery Plan (USFWS 2003), we created circular partitions with 0.8 km (0.5 mi) radii around each territory center. When two or more circular partitions would otherwise overlap, we used thiessen polygons to delineate territories used by each group. We hereafter refer to the resulting polygons as territory partitions. We tested whether the territory partitions encompassed the areas used by foraging groups of RCWs. After accounting for duration of observation session, we determined the proportion of sample points occurring within a group's territory partition, and we used a generalized linear mixed model (GLMM) with binomial errors and a logit link function and with territory ID as a random effect to model the proportion of points occurring within a group's territory partition as a function of the area of that group's territory partition and season. The significance of area or season was evaluated by removing each in turn and comparing the difference in deviance between the resultant model and the full model, and differences among seasons were compared using multiple contrasts.

Resource selection analysis

To evaluate resource selection, we imported RCW movement information into a geographic information system (GIS; ArcGIS, ESRI, Redlands, CA). Each observed RCW movement path was compared with 10 random movement paths. Random movement paths were simulated by rotating the track of points collected during each observation session around the territory center. Random tracks were rotated in 10 random orientations. The randomly rotated tracks produced comparable paths with the same general shapes of travel and the same relationships between individual locations and territory centers (i.e., accounted for tendencies of central place foragers; Rosenberg and McKelvey 1999). We used ArcMap version 10.0 to associate spatial information from the RCW Matrix Application and the Eglin Foraging Model with the simulated random and actual RCW movements. Five habitat metrics were also drawn from each observed and random location: the number of small hardwood stems/ha in the associated stand (10.2-25.4 cm [4-10 in] dbh), the number of medium hardwood stems/ha (25.4-35 cm [10-14 in] dbh), the number of large hardwood stems/ha (> 35 cm [14 in] dbh), the number of small pine stems/ha (10.2-25.4 cm [4-10 in] dbh), and the number of large pine stems/ha (> 25.4 cm [10 in] dbh). Note that we combined the numbers of pine stems in the 25.4-35 cm (10-14 in) and > 35 cm (14 in) size classes because very few pines > 35 cm (14 in) were present on Eglin AFB, despite the fact that Eglin has an unusually large number of old growth pines (i.e., > 200 years old) compared to most other landscapes in the Southeast. For each observed and random point we also calculated the distance to territory center.

We developed resource selection functions by comparing used points (given a value of 1) to random points (given a value of 0) with binomial GLMMs (Koper and Manseau 2012). Models included binomial error distributions and logit link functions. Data points collected from individual RCW groups were not independent, so we also added season and territory ID as random effects in all models (Gillies et al. 2006). Note that a RCW group on a given territory was never observed more than once in the same season, precluding the need to include observation session number as an additional random effect. In addition to a null model with only random effects, we constructed four categories of models according to their fixed effect predictor variables: 1) those with stand-level RCW Matrix Application scores as predictors; 2) those with Eglin Model score of habitat patches as predictors; 3) those with stand-level hardwood densities as predictors, and; 4) those with stand-level pine densities as predictors (Table 7).

We also examined potential interactions between predictor variables and group size and between predictor variables and distance to territory center to test whether the strength of resource selection differed as a function of group size or location within the territory. Thus, for each category of predictor variable, we constructed four types of models: those with no interactions, those with interactions between predictors and group size, those with interactions between predictors and distance to territory center, and those with both types of interactions (Table 7). We mean-centered all variables prior to resource selection analysis by subtracting values by their means so that main effects would remain biologically interpretable when involved in interactions (Schielzeth 2010). We ranked models using Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) and used the difference in AIC_c between the top model and other candidate models (ΔAIC_c) to calculate model weights (w_i). We considered models with $\Delta AIC_c < 2$ to be competing models (Burnham and Anderson 2002). To account for serial autocorrelation and differences in correlation structure between observed and random points, we followed the conservative approach of Koper and Manseau (2012) and report empirical standard errors of parameter estimates. Empirical standard errors are robust to the lack of independence among data points and are generally larger than model-based standard errors (see Koper and Manseau 2009). We used *k*-fold cross-validation to assess the fit of our resource selection functions (Koper and Manseau 2012). Based on slope estimates and confidence intervals from a regression of predicted selection versus observed selection, our models provided good predictive ability (Howlin et al. 2003).

We used SAS version 9.3 (SAS Institute Inc., Cary, North Carolina, USA) to obtain empirical standard errors and R version 3.0.0 (R Development Core Team 2013) for all other statistical analyses. We computed variance inflation factors (VIF) of all fixed effects in GLMMs and did not detect any multicollinearity (all VIF < 1.3), and full models did not show evidence of correlations among main effects (all $r < |0.32|$). We tested full models for overdispersion using a Pearson χ^2 test statistic and did not detect any overdispersion (all $p > 0.4$)

Table 7. Predictor variables included in GLMMs for resource selection. Four categories of models were created based on their predictor variables, and each category of model contained four types of models based on which interaction effects were included. Colons denote interaction effects. All models included season and territory ID as random effects. Variable codes follow those from Table 2 with the exception of PTPA.25 (number of pine stems/ha > 25.4 cm [10 in] dbh), GroupSize (RCW group size) and CenterDist (distance to territory center).

Model category	Predictor variables
RCW Matrix Application score models	RCW Matrix Score
	RCW Matrix Score + RCW Matrix Score × GroupSize
	RCW Matrix Score + RCW Matrix Score × GroupSize + RCW Matrix Score × CenterDist
	RCW Matrix Score + RCW Matrix Score × GroupSize + RCW Matrix Score × CenterDist
Eglin Foraging score models	Eglin Model Score
	Eglin Model Score + Eglin Model Score × GroupSize
	Eglin Model Score + Eglin Model Score × CenterDist
	Eglin Model Score + Eglin Model Score × GroupSize + Eglin Model Score × CenterDist
Hardwood density models	HTPA.10.25 + HTPA.25.35 + HTPA.35
	HTPA.10.25 + HTPA.25.35 + HTPA.35 + HTPA.10.25 × GroupSize + HTPA.25.35 × GroupSize + HTPA.35 × GroupSize
	HTPA.10.25 + HTPA.25.35 + HTPA.35 + HTPA.10.25 × CenterDist + HTPA.25.35 × CenterDist + HTPA.35 × CenterDist
	HTPA.10.25 + HTPA.25.35 + HTPA.35 + HTPA.10.25 × GroupSize + HTPA.25.35 × GroupSize + HTPA.35 × GroupSize + HTPA.10.25 × CenterDist + HTPA.25.35 × CenterDist + HTPA.35 × CenterDist
Pine density models	PTPA.10.25 + PTPA.25
	PTPA.10.25 + PTPA.25 + PTPA.10.25 × GroupSize + PTPA.25 × GroupSize
	PTPA.10.25 + PTPA.25 + PTPA.10.25 × CenterDist + PTPA.25 × CenterDist
	PTPA.10.25 + PTPA.25 + PTPA.10.25 × GroupSize + PTPA.25 × GroupSize + PTPA.10.25 × CenterDist + PTPA.25 × CenterDist

2.3 RESULTS

Our dataset consisted of 451 observation sessions at 97 woodpecker territories for a total of 37,109 GPS points. Each territory was monitored 1-9 times (mean ± SD = 4.6 ± 2.0). Mean duration of observation sessions was 88 min and ranged from 15-176 min.

Space use analysis

Mean maximum distance traveled by a group during the sessions was 431 m [0.27 mi], and distances ranged from 80-1,295 m [0.05-0.8 mi]. Maximum distance increased with duration of observation session ($R^2 = 0.09$, $t_{449} = 6.65$, $p < 0.001$; Fig. 19), indicating that birds generally moved away from the cluster center as they traveled. To account for the increase in maximum distance that was associated with session duration, our analysis of maximum travel distance and the evaluation of the proportion of points within the territory partition were restricted to sessions lasting > 110 min, a time which appeared to signify maximum movement distances (Fig. 19). However, except where noted below, results were similar when all observation sessions were included. Sessions with > 110 min of observations had a mean maximum distance traveled of 479 m [0.3 mi], and distances ranged from 111-1,012 m [0.07-0.6 mi]. Since the first 10 min of observation sessions were excluded and sessions always began within a group's home territory partition (see above), maximum distance after 110 min is essential equal to that after 2 hr.

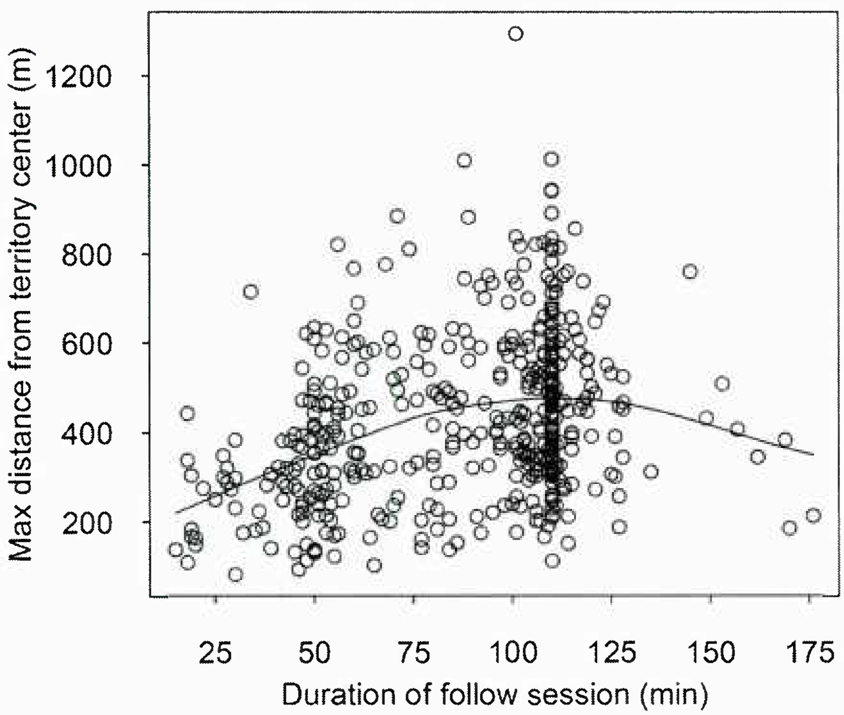

Figure 19. Relationship between duration of observation session and maximum distance traveled by a red-cockaded woodpecker group from its territory center. Curve was produced by loess smoothing with a smoothing parameter of 2/3 and a first degree polynomial.

After restricting our analysis to observation session that lasted at least 110 min, maximum distance tended to be shortest in spring but longest in summer and winter ($F_{3,148} = 4.5$, p =

0.0047, Tukey HSD, Winter-Spring: $p = 0.006$, Summer-Spring: $p = 0.048$, for all other comparisons $p > 0.05$; Fig. 20).

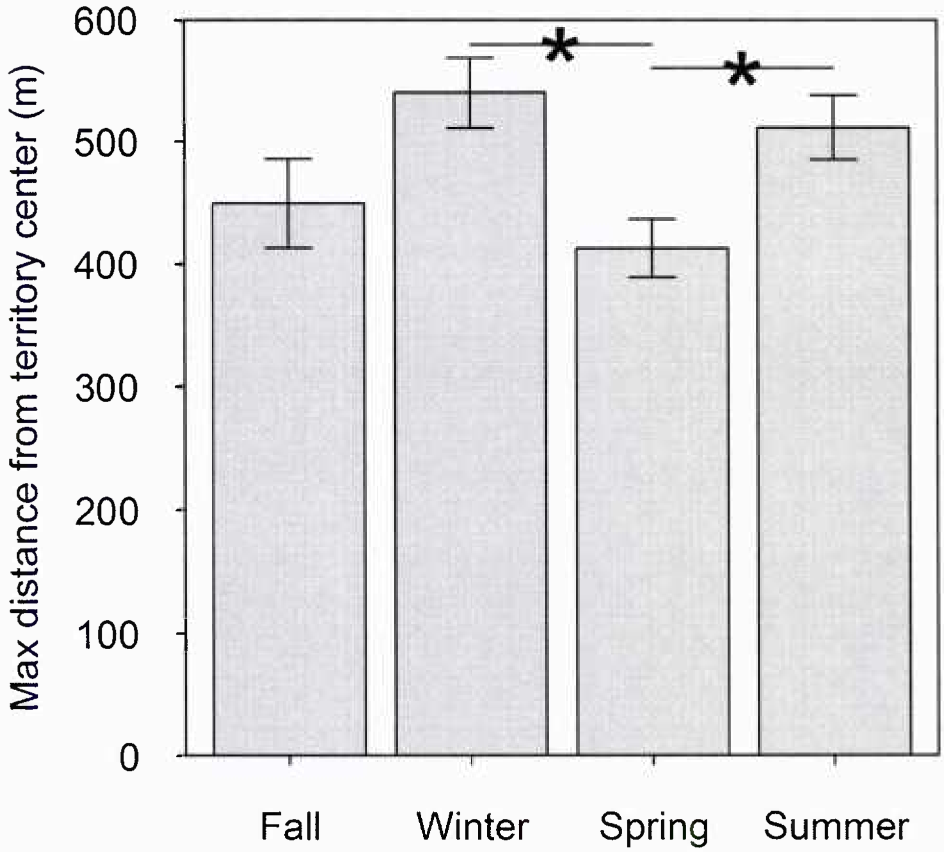

Figure 20. Mean maximum distance (± SE) traveled by RCW groups from their territory partition center in each season. Maximum distance was shortest in spring. Asterisks show significant differences.

Home territory partitions encompassed all of the foraging movement observations for most (63%) observation sessions (Fig. 21). However, there were several exceptional cases in which as few as 1/111 points occurred within a group's territory partition and 18 sessions in which fewer than 50% of points occurred within a group's territory partition. Two representative examples are shown in Figure 22. In one example, most points in the observation session occurred outside of the group's territory partition (Fig. 22a), whereas in the other example, all points occurred within the group's territory partition (Fig. 22b). Groups with territory partitions of smaller areas had fewer points occurring within their home territory partition ($\chi^2 = 28$, $p < 0.001$). Season also affected the proportion of points within a group's territory partition ($\chi^2 = 458.3$, $p < 0.001$), with more points occurring within a group's territory partition in spring, followed by fall, summer, then winter (Winter – Summer: $p = 0.02$, all other comparisons $p < 0.001$). Results were very similar when using all data points (i.e., not restricting to observation sessions lasting > 110 min), except that the difference in proportion of points within a group's home territory partition between winter and summer was no longer significant ($p = 0.99$).

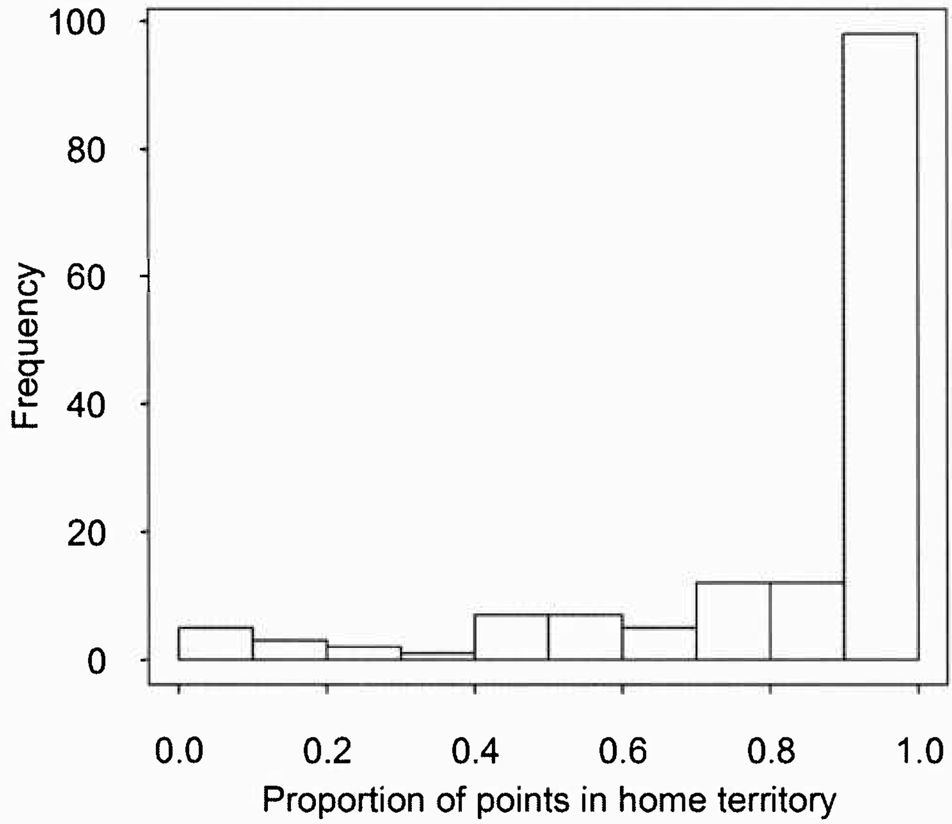

Figure 21. Frequency histogram of the proportion of points occurring within a red-cockaded woodpecker group's territory partition, after restricting analyses to observation sessions lasting at least 110 min.

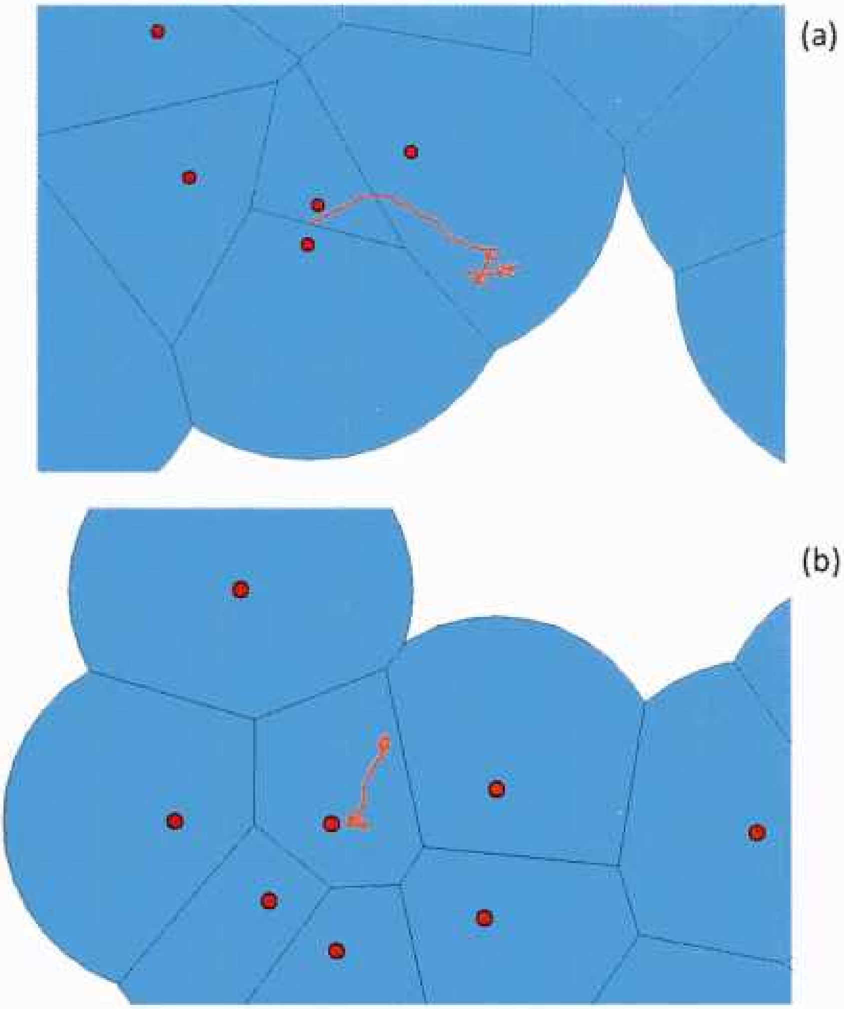

Figure 22. Two sample paths taken by RCW groups at Eglin AFB. Red dots indicate territory centers, which were derived from the mean coordinates of cluster trees. Territory partitions are delineated by the surrounding thiessen polygons, and tracks followed by foraging woodpecker groups are show in red. In (a), only 10/111 sample points occurred within the group's territory partition; in (b), all 111 sample points occurred within the group's territory partition.

Resource selection analysis

Model selection results indicated that the best approximating resource selection model included main effects of stand-level small (10.2-25.4 cm [4-10 in] dbh) and large (> 25.4 cm [10 in] dbh) pine stems/ha, interactions between group size and both sizes of pine trees, and interactions between distance to territory partition center and both sizes of pine trees (Table 8). No competing models were identified, and the second-ranked model in our analysis was substantially less plausible than the top ranked model ($\Delta AIC_c = 39.1$). Parameter estimates and empirical standard errors from the best approximating model indicated that RCW groups selected against stands with more small pine stems/ha ($\beta = -0.009 \pm 0.003$, $p < 0.001$), and RCW groups selected for stands with more large pine stems/ha ($\beta = 0.023 \pm 0.005$, $p < 0.001$). The interaction between small pine stems/ha and distance to territory center was negative ($\beta = -3 \times 10^{-5} \pm 1.3 \times 10^{-5}$, $p = 0.029$), indicating that selection against stands with more small pine stems/ha was greater when RCW groups were farther from their territory partition center (Fig. 23a). Other interactions were non-significant (i.e., confidence intervals overlapped with zero) when assessed using empirical standard errors. However, considering the conservative nature of empirical standard errors and the fact that these interactions appeared in the best model, there was suggestive evidence that selection against stands with more small pine stems/ha was greater for larger groups ($\beta = -0.002 \pm 0.001$, $p = 0.216$; Fig. 23b), and selection for stands with more large pine stems/ha was greater for smaller groups ($\beta = -0.001 \pm 0.003$, $p = 0.625$; Fig. 23d) and when groups were farther from their territory partition center ($\beta = 4 \times 10^{-5} \pm 2 \times 10^{-5}$, $p = 0.067$; Fig. 23c).

Table 8. Summary of the top four models for resource selection in the red-cockaded woodpecker at Eglin AFB. The number of parameters (*K*), AIC_c value, difference in AIC_c between the model and the best model (ΔAIC_c), and model weights (w_i) are shown. Season and territory ID were included as random effects in all models.

Model	*K*	AIC_c	ΔAIC_c	w_i
Used ~ PTPA.10.25 + PTPA.25 + PTPA.10.25 × GroupSize + PTPA.25 × GroupSize + PTPA.10.25 × CenterDist + PTPA.25 × CenterDist	9	247743.5	0	1
Used ~ PTPA.10.25 + PTPA.25 + PTPA.10.25 × CenterDist + PTPA.25 × CenterDist	7	247782.5	39.1	0
Used ~ PTPA.10.25 + PTPA.25 + PTPA.10.25 × GroupSize + PTPA.25 × GroupSize	7	247841.6	98.1	0
Used ~ PTPA.10.25 + PTPA.25	5	247908.2	164.7	0

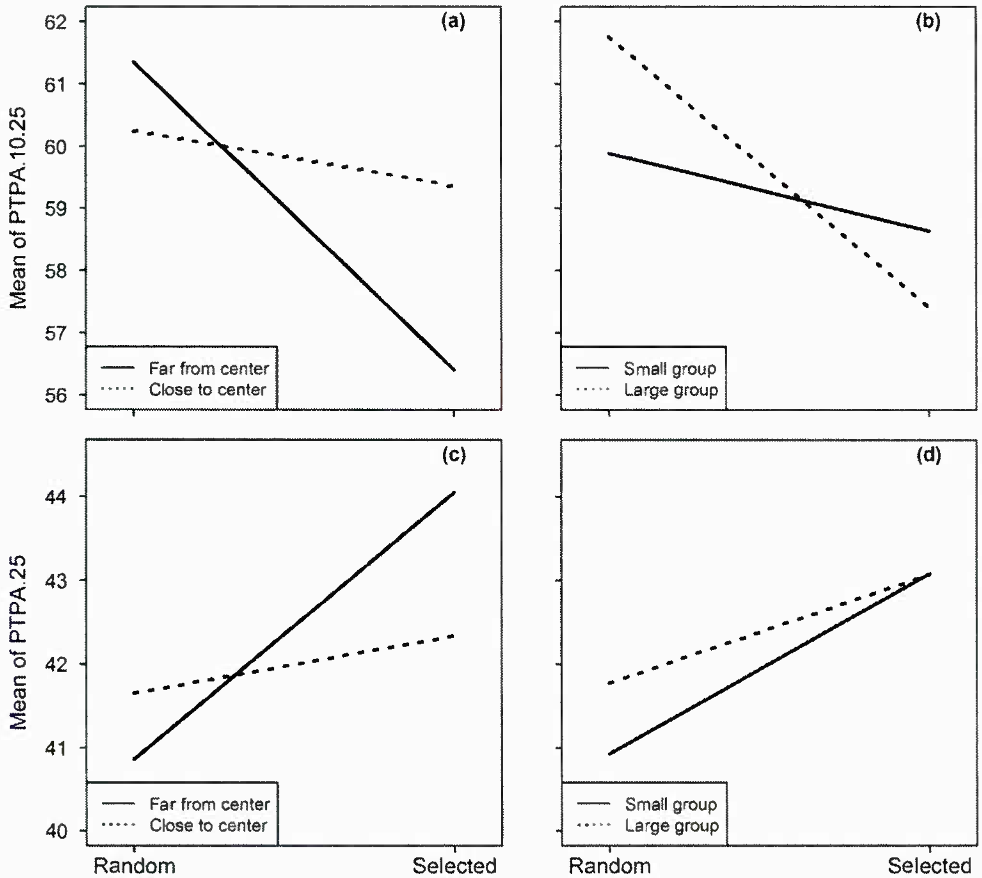

Figure 23. Interaction effects in resource selection models for foraging red-cockaded woodpeckers at Eglin AFB. Shown is the mean (a), (b) number of pine stems/ha 10.2-25.4 cm (4-10 in) dbh for random and selected points and (c), (d) number of pine stems/ha > 25.4 cm dbh (10 in) for random and selected points. For visualisation purposes, distance from territory partition center was separated based on points above ("far from center") and below ("close to center") the overall mean, and group size was separated based on those with >= 5 adults ("large group") and < 5 adults ("small group").

2.4 DISCUSSION

Using a large dataset of group follows Eglin AFB, we quantified space use and resource selection in foraging groups of red-cockaded woodpeckers. Many groups foraged entirely within their territory partitions, as defined following the USFWS Recovery Plan (USFWS 2003), and groups tended to travel shorter distances in spring but longer distances in winter and summer. In general, woodpeckers selected forest stands with more large pine stems/ha and fewer small pine stems/ha, but strength of selection differed according to group size and to the group's relative position within the territory.

Foraging RCWs traveled as far as 1,295 m [0.8 mi] from their territory partition center, with a mean maximum distance of 479 m [0.3 mi] for groups followed for two hours. The majority of observation sessions occurred entirely within a group's territory partition (Fig. 21), indicating that thiessen polygons that are widely used by managers to represent RCW foraging areas reasonably reflected the foraging space. Similarly, Convery and Walters (2004) found that territory partitions encompassed on average 80% of the actual home range used by RCWs at Marine Corps Base Camp Lejeune, North Carolina. However, in that study there was considerable variation among groups, with 17% of groups having less than 70% of their home range encompassed by their territory partitions. Accordingly, we found that during 18 observation sessions fewer than 50% of observed RCW locations occurred within the home territory partition (Fig. 21), indicating that in certain circumstances, thiessen polygons are not fully representative of the space used by some RCW groups. Ineffective thiessen polygons were often identified in areas that were charaterized by high densities of cluster trees and territories, which casued oddly-shaped and small territory partitions. Indeed, those 18 observation sessions with fewer than 50% of points occurring within a group's territory partition had smaller territory sizes (mean ± SD = 84.2 ± 45.6 ha [208 ± 113 ac]) than the 134 sessions with more than 50% of points occurring within the partition (101.8 ± 32.4 ha [252 ± 80 ac]). Figure 22 provides an example of a RCW group on a smaller territory that foraged primarily outside of its home partition, and a group with a larger territory that spent the entire session within its home partition. Thus, we recommend that empirical observations of home ranges be performed in high density areas in order for managers to accurately assign habitat to particular groups.

After accounting for duration of observation session, and individual territory heterogeneity, maximum travel distance from the territory center was shortest in spring (Fig. 20). Similarly, Skorupa and McFarlane (1976) and Bradshaw (1990) found foraging ranges to be significantly larger in winter when compared to ranges used in the nesting season in South Carolina and Virginia, respectively. Two mechanisms could account for the observed pattern. First, the presence of eggs or nestlings in spring likely reduces travel distance as adults must return to the nest cavity to incubate or feed the young (Ligon 1970). Second, energetic demands are likely higher in winter due to cooler temperatures and longer nights. Also, food availability is likely reduced during winter as cooler temperatures reduce arthropod activities, which may force groups to forage more widely. Seasonal prey availability also has been suggested to contribute to the increased use of hardwoods for foraging in winter in certain RCW populations (Skorupa and McFarlane 1976; DeLotelle et al. 1987). Accordingly, we also found that the proportion of points within a group's territory partition was smallest in winter. Interestingly, maximum travel distance was second-highest in summer, and the second-lowest proportion of points occurred within a group's territory partition in summer. These findings suggest that the presence of fledglings in a group may increase its energy demands, resulting in larger foraging area requirements in summer. Taken together, our results indicate that RCW foraging area requirements are largest in winter and second-largest in summer, and that season, along with territory aggregation (density) and the resulting reduction in area of territory partitions, should be taken into account when assessing the spatial requirements of RCW groups.

Our results parallel previous research on resource selection in RCWs (Hardesty et al. 1997; Doster and James 1998; Walters et al. 2002), in that RCW groups at Eglin AFB selected forest stands with more large (>25.4 cm [10 in] dbh) and fewer small (10.2-25.4 cm [4-10 in] dbh) pine stems/ha. Resource selection models including variables for large and small pine stem densities received substantially more support than models with RCW Matrix Application scores, Eglin Foraging Model scores, or hardwood densities as predictor variables (Table 8). These results could reflect several key issues. Stand-level RCW Matrix Application scores might not have accurately reflected stand quality at Eglin AFB because key input components of the Application, herbaceous groundcover and fire data, were missing. Thus, other forest metrics, possibly of less importance, were re-weighted in the model. In addition, Eglin AFB is characterized by few large pines – for example, mean PTPA.35 on all territories monitored was only 7 stems/ha – and RCW Matrix scores were likely reduced as a consequence. The Eglin Foraging Model makes use of remote sensing to establish scores for hexagonal habitat patches of 1 ha (2.5 ac). Scores are presumably based on longleaf pine basal area, and resource selection models with Eglin Foraging Model scores may thus have been somewhat redundant to models with pine stems/ha as predictor variables. Further, the small size of hexagons, in comparison to forest stands, and the small range of possible scores (0-3), may have contributed to the lack of association between habitat selection by foraging woodpeckers and Eglin Foraging Model scores. Finally, hardwood models may not have received support because, as discussed in Part 1 (section 1.5), RCWs may be more tolerant of a range of hardwood densities on restored habitats than was previously thought (see also Hiers et al. In press). Correlation among habitat metrics precluded us from constructing models with both pine and hardwood components in the same model, and so it remains possible that RCW groups at Eglin AFB selected stands based on hardwood metrics in addition to pine metrics.

Selection for stands with higher densities of large pine trees and lower densities of small pine trees appeared to vary based on group size and distance to territory center (Fig. 23). In particular, selection against areas with high densities of small pines was stronger when groups were farther from their territory center and for larger groups, and selection for areas with high densities of large pines was stronger when groups were farther from their territory center and for smaller groups; though note that only the first association was significant when using empirical standard errors. Relationships between strength of resource selection and location within the territory align with the predictions of optimal foraging theory, which suggests that greater foraging rewards must be obtained at greater distances, in order to overcome the elevated costs of transit (MacArthur and Pianka 1966). Selection also might have been stronger when groups were farther from their territory center because stand quality could decrease as a function of distance from the cluster core. The interaction between group size and pine densities is somewhat more difficult to explain. On the one hand, larger groups might be less selective than smaller groups, as was found for selection for stands with more large pine stems/ha, because coordinating the movements of a large group might be hindered by the many ongoing social interactions, especially if fledglings are part of the group. On the other hand, larger groups might be more selective than smaller groups, as was found for selection against stands with more small pine stems/ha, because the foraging requirements of larger groups are greater. In any case, further research is needed to identify the mechanisms leading to differences in the strength of resource selection among varying group sizes.

In summary, our results indicate that territory partitions, as they are currently used in RCW management, reasonably encompassed the foraging space used by RCW groups at Eglin AFB, but that particular care should be taken when interpreting the space used by groups on territories that are small due to dense aggregations of cluster centers. Collecting empirical home range data and perhaps including territory partitions with partial overlap among aggregated territories would be a useful alternative to thiessen polygons. We also found that densities of large and small pine trees were more useful indicators of stand selection than were the RCW Matrix Application scores of stands or the Eglin Foraging Model scores of habitat patches. However, our results should not be used to discount the utility of the foraging models in predicting foraging habitat quality because performance may have been impeded by missing input data for Eglin AFB. Groundcover often shows the strongest association with RCW fitness (see Part 1; Hardesty et al.

1997; James et al. 1997, 2001), and so including groundcover data, or fire history as a surrogate, would likely improve the performance of habitat models. Finally, we emphasize the importance of studying RCW habitat use and resource selection on restored landscapes, which may reveal insights into the range of habitat conditions acceptable for RCWs, as indicated by our findings for hardwoods. Of course, resource selection alone does not necessarily reflect bird fitness, and so combining selection with measures of reproduction and survival would no doubt result in improved foraging guidelines.

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APPENDIX

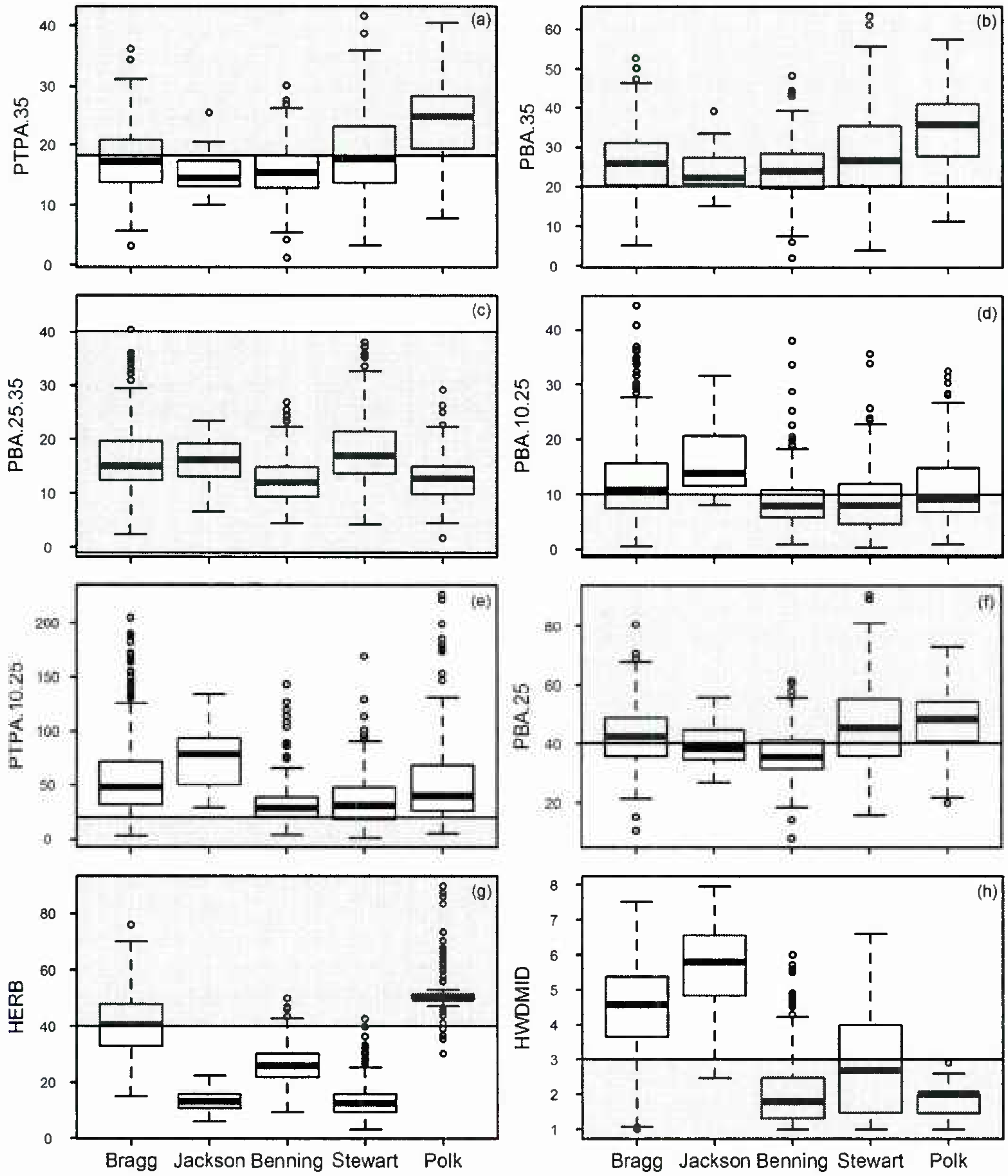

Figure S1. Variation in eight foraging habitat metrics used to define good quality foraging habitat for the red-cockaded woodpecker (Table 2, USFWS 2003). Shown are the median, interquartile range and outliers for habitat metrics on territories at each of five military installations where standardized forest inventory data were collected. Shaded areas indicate the range of values considered good quality foraging habitat according to the Recovery Plan guidelines. Units are ft^2/ac for basal area and stems/ac for tree density. See Table 2 for variable descriptions.

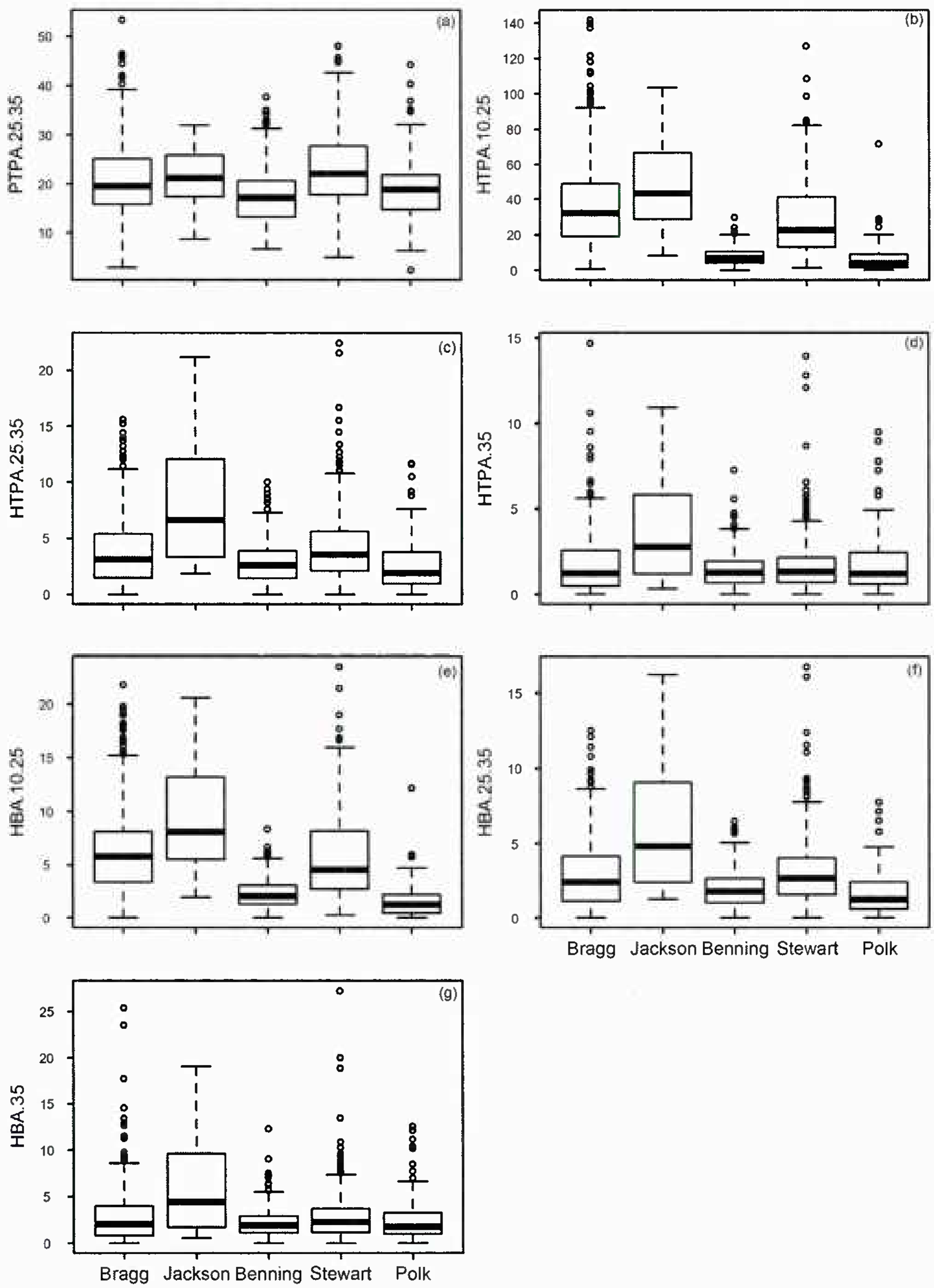

Figure S2. Variation in seven additional habitat metrics used in our study at each of five military installations where standardized forest inventory data were collected. Shown are the median, interquartile range and outliers for habitat metrics on territories at each of five military installations. Units are ft^2/ac for basal area and stems/ac for tree density. See Table 2 for variable descriptions.

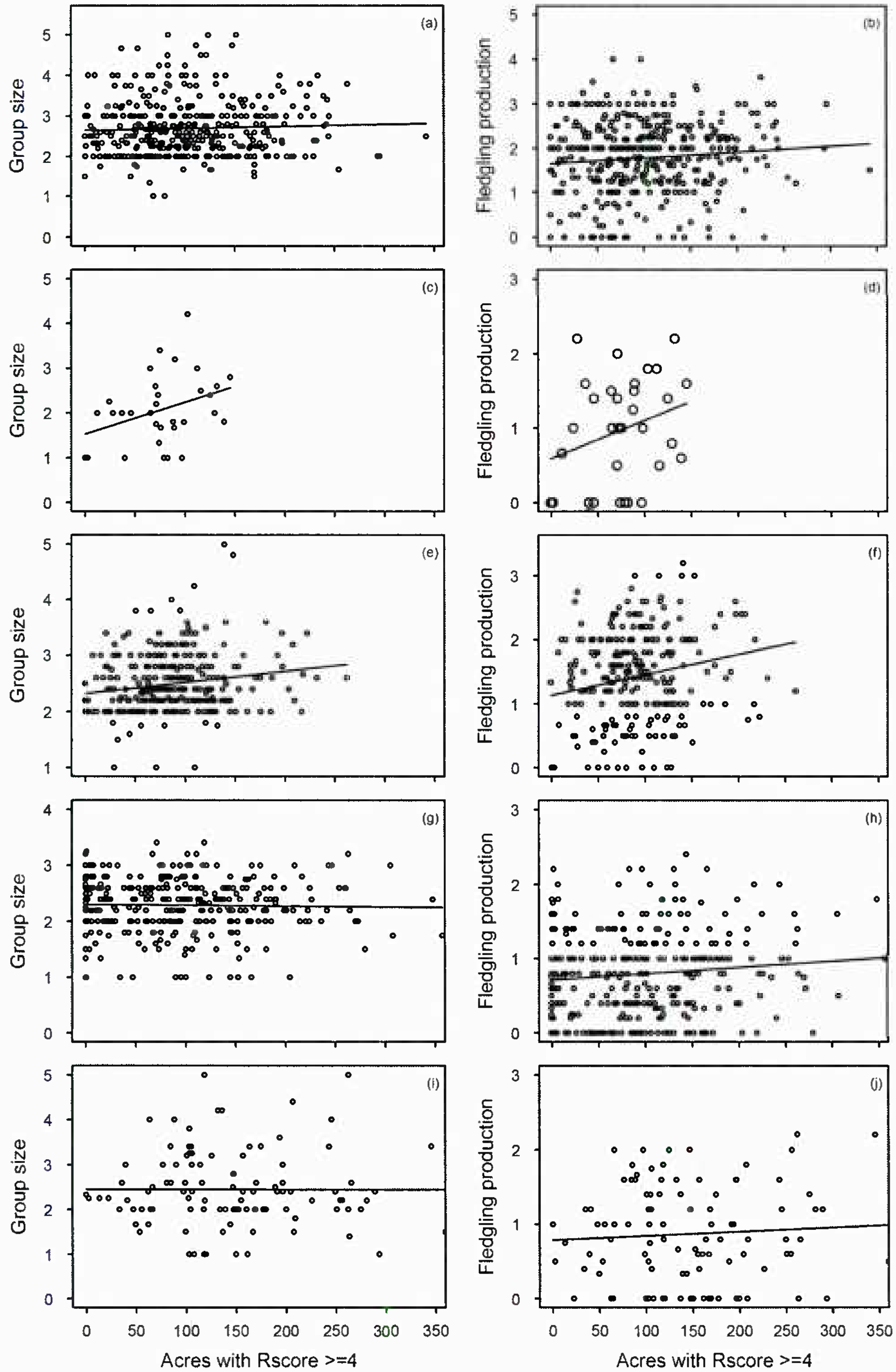

Figure S3. Relationship between mean group size or fledgling production and number of hectares with a Recovery Standard score >= 4 as assessed by the RCW Foraging Matrix Application for individual territories at five military installations: (a), (b) Fort Bragg, (c), (d), Fort Jackson, (e), (f), Fort Benning, (g), (h), Fort Stewart, (i), (j), Fort Polk.