Biological Conservation 175 (2014) 52–64

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Geographic variation in fitness and foraging habitat quality in an endangered bird

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ARTICLE INFO

Article history:
Received 7 January 2014
Received in revised form 31 March 2014
Accepted 2 April 2014

Keywords:
Fitness
Fledgling production
Foraging habitat
Group size
Model
Picoides borealis
Red-cockaded woodpecker

ABSTRACT

Models are important tools for conservation, but the usefulness of any given model for decision-making depends on its accuracy and precision. Few models designed for conservation purposes are validated with real-world data, and such models are even less likely to be revisited and improved with post-implementation results. We test the performance of a model frequently used and heavily relied-upon for the management of the endangered red-cockaded woodpecker (*Picoides borealis*). The RCW Foraging Matrix Application incorporates spatially-explicit forest stand data and woodpecker territory locations to produce quantitative assessments of foraging habitat quality. Model parameters were based on expert opinion and research performed on several key populations at a time when range-wide habitat quality was relatively poor. Since the model's inception, many red-cockaded woodpecker populations have been monitored intensely in restored habitat, providing an opportunity to evaluate model performance range-wide. We assessed the relationship of habitat quality, as measured by the RCW Matrix Application, to group size and fledgling production from populations across the species range in the southeastern United States. We also evaluated foraging habitat quality directly by relating woodpecker fitness components to foraging habitat metrics through regression tree analyses. Results showed that some, but not all, of the habitat metrics included in the RCW Matrix Application were consistently related to fitness components range-wide, but threshold values for these habitat metrics identified by regression tree analyses were site-specific rather than universal. Our findings indicate opportunities for improving on "one-size-fits-all" range-wide models with analyses of additional locally-relevant foraging habitat metrics.

1. Introduction

Models are important tools for endangered species management and conservation (Beissinger et al., 2006). Models can also allow conservationists and managers to explore the consequences of understandings of biological systems. Examples include the use of population viability analysis to assess species vulnerability to extinction (Brook et al., 2000), bioclimatic niche models to predict range shifts under future climate change (Carroll, 2010), and spatially-explicit habitat models to evaluate population responses to changes in landscape conditions or management policies (Liu et al., 1995; McFarland et al., 2012). As increases in computing power continue to improve model realism, there will likely be increased reliance on models for policy and decision-making.

The usefulness of any particular model for decision-making depends on its accuracy and precision, and on the needs of conservationists. Ecological models are, by definition, simplified representations of natural systems, and most rely on field data for both parameterization and validation. However, few models built for conservation purposes are ever validated with real-world data (Collier et al., 2012; McCarthy et al., 2000; O'Connor and Wagner, 2004; Schiegg et al., 2005). Even rarer are cases in which such models are revisited and improved with real-world data (Mitchell et al., 2001; Schiegg et al., 2005). Yet, unrealistic models derived from limited data can lead to unreliable estimates and poor management decisions (Beissinger and Westphal, 1998).

Model validation involves comparing model predictions to actual population performance, which can be conducted in several ways. One method for assessing how well a model generalizes across time is to develop a model based on a particular population and then test predictions with that same population's performance

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http://dx.doi.org/10.1016/j.biocon.2014.04.007
0006-3207/

during a different time period (Brook et al., 2000). A model's ability to generalize across space can be evaluated by parameterizing a model with data from one region and testing how well the model predicts conditions in another region (Carroll et al., 1999; McCarthy et al., 2000; Schiegg et al., 2005). Finally, certain types of models may only be amenable to having secondary model predictions validated with field data (McCarthy et al., 2001).

The red-cockaded woodpecker (*Picoides borealis*) is an endangered species that has received considerable conservation investment, including the development of ecological and conservation-oriented models to facilitate management decision-making. We here test the performance of a model frequently used to assess red-cockaded woodpecker foraging habitat quality. In doing so, we incorporate aspects of model validation described above, including a comparison of model predictions and observed outcomes, a comparison between time periods, and an assessment of model performance across space involving multiple populations. We additionally evaluate how the model might be improved through localized assessments of fitness components (group size and fledgling production) and variation in foraging habitat quality.

1.1. Red-cockaded woodpeckers

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, remnant populations occur throughout most of the species' historic range (Fig. 1). Three major factors contributed to drastic population declines over 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 contributed further to habitat degradation, as red-cockaded woodpeckers are cooperative breeders that excavate roosting and nesting sites in live mature pines (Jackson et al., 1979). The abundance of such cavities has been shown to be a driver of population processes (Walters et al., 1992). Third, fire suppression across the region allowed the development of dense hardwood midstories that shaded out the diverse ground cover that historically characterized these pine systems (Peet and Allard, 1993), reducing foraging habitat quality.

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 productivity. Larger group sizes, which generally indicated higher-quality territories (Conner et al., 2001), and greater fledging production, were related to habitat features that included 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 to produce habitat quality scores (later updated 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 (Tables A1, A2 – Appendix A). These evaluations can be used to assess the impacts of projects that may cause the loss

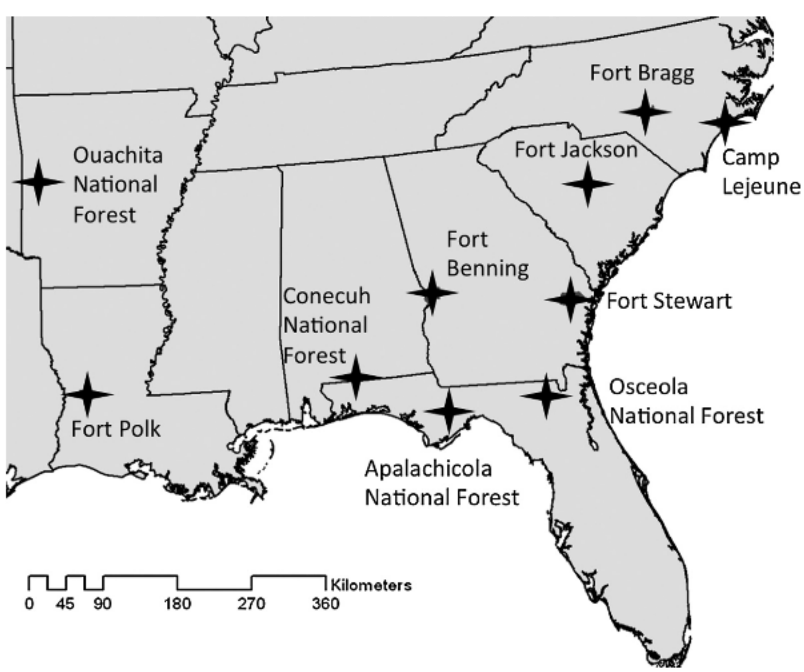

Fig. 1. Sampling locations for an analysis of fitness and foraging habitat quality in the red-cockaded woodpecker.

(e.g., via development), temporary removal (e.g., harvesting followed by restoration), or modification (e.g., pine thinning) of red-cockaded woodpecker foraging habitat. These factors are particularly relevant to military installations where forest stands are often managed for multiple uses including timber harvest.

The research that led to the development of the RCW Matrix Application was based mostly on comparisons of fire-suppressed habitat to the limited amounts of fire-maintained habitat that existed at the time. Red-cockaded woodpecker populations have since increased in a variety of fire-maintained areas, many of which differ in attributes such as pine density, abundance of hardwoods, and ground cover condition. Due to the bird's protected status the red-cockaded woodpecker has been intensely monitored at many sites. United States military installations have been instrumental in monitoring and recovery due to their large area, intensive habitat management, commitment to recovery, and possession of some of the last remaining longleaf pine habitats. United States National Forests also have numerous substantial woodpecker populations that have been extensively monitored, and in some cases intensively managed (USFWS, 2003). Woodpecker demographic data from these sites allowed us to examine range-wide variation in group size and fledgling production. Further, a subset of sites with both demographic and habitat data provided a unique opportunity to examine range-wide variation in foraging habitat quality and the effectiveness of the early foraging habitat guidelines in increasing group sizes and fledgling production across the range of restored habitats that now exist. Our objectives were to (1) summarize recent range-wide variation in woodpecker fitness components (group size and fledgling production) and foraging habitat metrics; (2) evaluate the performance of the RCW Matrix Application for predicting woodpecker fitness components; and (3) examine range-wide variation in foraging habitat quality by using regression tree analyses to identify site-specific features, and condition thresholds, which were related to group size and fledgling production.

2. Methods

2.1. Study area

We collected red-cockaded woodpecker demographic data from two military installations, 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 Forest (NF) populations, 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 a 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, encompassing much of the species' current distribution across the Coastal Plain and Piedmont regions of the southeastern United States (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 (*Pinus taeda*) and shortleaf pine (*Pinus echinata*), with some slash pine (*Pinus eliottii*). Groundcover was composed mainly of wiregrasses (*Aristida stricta* and *Aristida 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 red-cockaded woodpeckers, with the exception of Fort Polk, which included two populations separated by approximately 30 km. Fort Polk sites were similar in habitat and were pooled for analysis. Our analysis of woodpecker fitness components included a total of 1944 active territories, and our analyses of foraging habitat included a total of 1283 active territories (Table 1).

2.2. Group size and fledgling production

Red-cockaded woodpeckers are non-migratory and occupy year-round territories as solitary males, pairs, or cooperatively breeding groups (Jackson, 1994; Walters et al., 1988, 1992). 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 non-breeding helpers, which are typically offspring fledged during previous breeding seasons (Conner et al., 2001).

Two fitness components were used to reflect the suitability and productivity of territories: group size and the number of fledglings produced. Higher-quality territories have been shown to host larger groups of birds (Conner et al., 2001), and productivity is thought to be associated with territory quality, although it also has been associated with the age of dominant birds and number of helpers (Conner et al., 2001; Heppell et al., 1994). Group size and fledgling production tend to be positively correlated, but we chose to analyze relationships between habitat features and each fitness component separately because we were interested in identifying habitat features and thresholds associated with either aspect of fitness. Habitat features selected by adults do not necessarily translate to greater offspring survival (Walters et al., 2002), and factors other than group size (e.g., nest predation pressure) can influence productivity. Similarly, factors that may be independent of productivity (e.g., adult survival) can influence group size. Moreover, in rapidly-growing recovery populations with abundant cavity resources, the relationship between group size and fledgling

Table 1
Study sites used in range-wide analyses of red-cockaded woodpecker fitness components (all sites) and foraging habitat quality (Fort Bragg, Fort Jackson, Fort Benning, Fort Stewart, and Fort Polk). Available territories were defined as those occupied by at least one adult in at least one year of the 5-year study period, and area was calculated as the summed area of all territories at a site (see Section 2.3).

Site (years)	Location	Ecoregion	Available territories	Area (1000 ha)
Fort Bragg (2008–2012)	NC (79.30°E, 35.11°N)	Sandhills	391	37
MCBCL (2007–2011)	NC (77.34°E, 34.59°N)	Atlantic Coastal Plain	94	8
Fort Jackson (2008–2012)	SC (80.82°E, 34.04°N)	Sandhills	44	5
Fort Benning (2008–2012)	GA (84.97°E, 32.37°N)	Sandhills	376	36
Fort Stewart (2007–2011)	GA (81.61°E, 31.88°N)	Atlantic Coastal Plain	366	38
Apalachicola NF (2007–2011)	FL (84.67°E, 30.24°N)	Eastern Gulf Coastal Plain	312	32
Osceola NF (2008–2012)	FL (82.32°E, 30.29°N)	Atlantic Coastal Plain	149	15
Conecuh NF (2008–2012)	AL (86.64°E, 31.10°N)	Eastern Gulf Coastal Plain	43	4
Fort Polk (2008–2012)	LA (93.08°E, 31.07°N)	Western Gulf Coastal Plain	106	9
Ouachita NF (2008–2012)	AR (94.25°E, 34.50°N)	Eastern Gulf Coastal Plain	63	7

production may become decoupled when inexperienced birds that would otherwise remain as helpers, breed in new territories on their own. Indeed the correlation between the two fitness components in our data set is only modest (see below).

Group size and fledgling production at each territory were recorded at study sites 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. We used the maximum number of adults observed foraging together during the breeding period as the measure of 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 after a failed attempt, we used the number of fledglings from their final attempt. For groups that attempted a second nest following a successful first nest, an extremely rare occurrence (Phillips et al., 1998), we used the number of fledglings from 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 in at least one of the years of study. Years when no adults were present on a territory were not included in the calculation of mean group size and mean fledgling production.

2.3. Foraging habitat metrics and territories

Standardized forest inventory data appropriate for analysis with the RCW Foraging Matrix Application were available from five study sites. Data were provided 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 diameter at breast height [dbh], 25.4–35 cm dbh, and >35 cm dbh), percent of herbaceous groundcover, and an index of hardwood midstory (Table 2). The Red-Cockaded Woodpecker 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).

Cavity tree locations for each territory were provided from endangered species biologists at the above five sites. We defined territories by first calculating territory centers as the arithmetic mean of cavity tree coordinates, and we used ArcMap version 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) to create circular partitions of 0.8 km 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 groups of birds (Convery and Walters, 2004) and is the current method advocated by the U.S. Fish and Wildlife Service and used in the RCW Matrix Application to define territories. Hereafter, we use the term “territory” to represent the habitat area within partitions.

2.4. 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 (see Table A1 – Appendix A for a detailed description of how scores are calculated). In brief, the RCW Matrix Application provided a numerical score for recovery standard (Rscore) and a pass/fail score for managed stability (Mscore). For the recovery standard, scores (1–5, with 5 being the highest) were produced from individual stand-level evaluations of 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, 25.4–35, and >35 cm dbh), percent herbaceous groundcover, an index of hardwood midstory, percentage of canopy hardwoods, fire history, and stand age. The RCW Foraging Matrix Application weights and combines these variables to produce a score for each stand within a territory. 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 of the territory center, and contiguous foraging habitat within the territory were 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 scores can range from 1 to 5, overall territory Rscores tend to be lower (1–2.2 in our evaluations) because only stands that meet all standards set out in the Recovery Plan are considered GQFH. The standard for managed stability was 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 stands receiving a 1 in all categories and the basal area of pines >25.4 cm dbh within the territory were calculated and given a score of 0 or 1. The territory received a final Mscore of 1 (pass) if both territory-level requirements were met and 0 (fail) if any were not met.

2.5. Statistical analysis

We used multiple approaches to evaluate the relationship between RCW Matrix Application scores and woodpecker fitness components at the five sites where both fitness components and habitat metrics were available. First, we used linear regression to examine the relationship between RCW Matrix Application 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 Matrix Application 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 an Rscore 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). The approach provided a way to use group size and reproduction data for each site to identify conditions associated with higher and lower group sizes and numbers of fledglings produced. 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 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

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 of pines that are >60 years in age and >35 cm dbh. Minimum basal area for these pines is 4.6 m^2/ha	Mean number of pines stems/ha >35 cm dbh (PTPA.35)
	Mean pine basal area/ha >35 cm dbh (PBA.35)
(2) Basal area of pines 25.4–35 cm dbh is between 0 and 9.2 m^2/ha	Mean pine basal area/ha 25.4–35 cm dbh (PBA.25.35)
(3) Basal area of pines <25.4 cm dbh is below 2.3 m^2/ha and below 50 stems/ha	Mean pine basal area/ha 10.2–25.4 cm dbh (PBA.10.25) Mean number of pines stems/ha 10.2–25.4 cm dbh (PTPA.10.25)
(4) Basal area of all pines >25.4 cm dbh is at least 9.2 m^2/ha. That is, the minimum basal area for pines in categories (1) and (2) above is 9.2 m^2/ha	Mean pine basal area/ha >25.4 cm dbh (PBA.25)
(5) Groundcovers of native bunchgrass and/or other native, fire-tolerant, fire-dependent herbs total 40% 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 in height	Index of hardwood midstory[a] (HWDMID)
Other	Mean number of pine stems/ha 25.4–35 cm dbh (PTPA.25.35) Mean number of hardwood stems/ha 10.2–25.4 cm dbh (HTPA.10.25) Mean number of hardwood stems/ha 25.4–35 cm dbh (HTPA.25.35) Mean number of hardwood stems/ha >35 cm dbh (HTPA.35) Mean hardwood basal area/ha 10.2–25.4 cm dbh (HBA.10.25) Mean hardwood basal area /ha 25.4–35 cm dbh (HBA.25.35) Mean hardwood basal area/ha >35 cm 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.

Fabricius, 2000). Many previous analyses of foraging habitat for red-cockaded woodpeckers have used multiple linear regression (see Walters et al., 2002 for examples), which essentially identifies linear relationships between woodpecker fitness components and habitat features. However, our approach was unique in that regression tree analysis identifies breaks in patterns, or thresholds, at which ecological phenomena may occur. In other words, rather than concluding, for example, that more large pines are associated with larger woodpecker group sizes, we can state the threshold value for large pines at which larger woodpecker groups occurred. There was substantial variation among sites, so we chose to analyze data from each site separately to detect thresholds associated with localized fitness components and features. We also were concerned about inconclusive results from a pooled data set that included sites with different, or opposite, relationships between conditions and fitness components. Further, pooling data would have given more weight to larger populations (e.g., Fort Benning, Fort Bragg) and may have obscured important results for smaller populations (e.g., Fort Jackson).

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 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 ArcMap version 10.0 to identify forest stands within 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, 25.4–35, and >35 cm dbh), percent herbaceous groundcover, and an index of hardwood midstory. These included all habitat metrics listed in Table 2 with the exception of pine basal area/ha >25.4 cm dbh (PBA.25), which is simply the sum of pine basal area/ha 25.4–35 cm dbh (PBA.25.35) and pine basal area/ha >35 cm dbh (PBA.35). We built a total of 10 such models – one for each fitness component (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 regression 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). All statistical analyses were performed in R version 2.15.1 (R Development Core Team, 2012), and we used the 'rpart' package for regression tree analysis.

3. Results

3.1. Group size and fledgling production

Mean group size per site ranged from 1.90 to 2.96 adults and generally decreased in the south and west portions of the red-cockaded woodpecker range, though these geographic relationships were non-significant (Fig. 2a; 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 per territory ranged from 0.77 to 1.79, and also tended to be non-significantly lower in more southern and western sites (Fig. 2b; Fledgling production vs latitude: $R^2 = 0.29$, $t_8 = 1.82$, $p = 0.107$; Fledgling production vs longitude: $R^2 = 0.27$, $t_8 = -1.73$, $p = 0.122$). Similar to Conner et al. (2001), we found some evidence for higher productivity in more inland sites after controlling for latitude. For example, fledgling production was significantly higher at Fort Bragg compared to Camp Lejeune (all sites $F_{9,1823} = 53.5$, $p < 0.001$; Tukey HSD test, Bragg – Lejeune $p < 0.001$) and Fort Benning compared to Fort Stewart (Benning – Stewart $p < 0.001$). Across all sites, group size explained about 18% of the variation in fledgling production ($R^2 = 0.18$, $t_{1777} = 19.9$, $p < 0.001$).

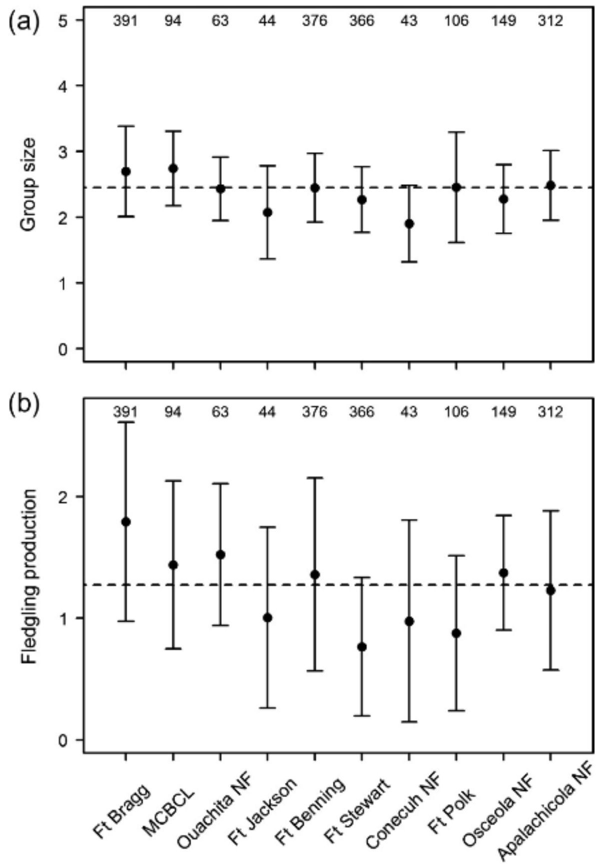

Fig. 2. (a) Mean annual group size ± SD and (b) fledgling production ± SD per territory calculated using each year that at least one adult red-cockaded woodpecker was present on a territory between 2007 and 2012. Sample sizes are shown above each point and dashed lines indicate the overall means. Sites are ordered by decreasing latitude.

3.2. Foraging habitat metrics

Forest metrics included in the Recovery Plan guidelines showed considerable variation across sites (Fig. 3). In particular, herbaceous groundcover (Fig. 3g) and hardwood midstory index (Fig. 3h) were quite variable, with the two north-eastern sites (Fort Bragg and Fort Jackson) exhibiting elevated hardwood components when compared to other sites. Similar patterns were found for the seven forest metrics not included in the Recovery Plan guidelines, with generally elevated hardwood density in the northeast, particularly among smaller size classes (Fig. A1 – Appendix A). Additionally 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 pine basal area for pines in the 25.4–35 cm dbh class (Fig. 3c), but very few were below the recommended maximum of 2.3 m^2/ha basal area with fewer than 50 stems/ha for pines in the 10.2–25.4 cm dbh class (Fig. 3d and e), and few were above the recommended minimum of 40% herbaceous groundcover (Fig. 3g).

3.3. RCW Foraging Matrix Application evaluations

Overall, RCW Matrix Application territory scores were not strong predictors of mean group size or fledgling production (Fig. 4 and 5). 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. 4b and 5b), 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. 4e and f). All other relationships between group size or fledgling production and Rscores or Mscores were non-significant.

Similarly, the percent of habitat within a territory that received an Rscore of greater than or equal to 4 was not strongly related to group size or fledgling production (Fig. A2 – Appendix A), though this relationship was significant and positive for group size and fledgling production at Fort Benning (Group size: $R^2 = 0.03$, $t_{302} = 3.11$, $p = 0.002$; Fledgling production: $R^2 = 0.04$, $t_{264} = 3.43$, $P < 0.001$), and for fledgling production at Fort Stewart ($R^2 = 0.01$, $t_{345} = 2.11$, $p = 0.036$).

3.4. Regression tree analysis

The top habitat metrics selected by regression tree analyses, and their numerical value, differed among sites and between fitness components (Table 3). We present a regression tree for Fort Bragg (Fig. 6), and the remainder are provided online (Figs. A3–A6 – Appendix A). 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 3). Greater numbers of stems/ha and higher basal area of large pines, and higher levels of herbaceous groundcover, were identified as important for fitness components at most sites, and either higher or lower amounts of small pines were identified at all sites. Herbaceous groundcover was most frequently associated with fledgling production, whereas pines were more frequently associated with group size (Table 3).

4. Discussion

We tested the performance of a model frequently used in the management of the endangered red-cockaded woodpecker by relating foraging habitat quality scores produced by the model to fitness components over the course of multiple years and across the species' range. Overall, scores from the RCW Foraging Matrix Application were not tightly linked to group size or fledgling production, though resulting relationships were generally in the expected direction (i.e., higher scores associated with higher group size or fledgling production), and there were several statistically significant associations (Figs. 4 and 5, Fig. A2 – Appendix A). We further identified locally-relevant foraging habitat metrics and associated thresholds that were related to higher or lower group size or fledgling production at each site (Table 3, Figs. A3–A6 – Appendix A).

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 measures of fitness (reviewed in Walters et al., 2002). Findings from this work were incorporated in the Recovery Plan guidelines for good-quality foraging habitat (USFWS, 2003) and in the development of the RCW Matrix Application, and yet we found only weak associations between habitat quality scores (Rscore and Mscore) and group size or fledgling production. There are several possible reasons for our failure to find the expected relationships between habitat quality scores and woodpecker fitness components. First and foremost, the Rscore and Mscore indices attempt to compress many features into single measures of complicated biological processes that may not be well represented by such simplifications. Similarly, the spatially explicit analyses conducted by the RCW Matrix Application may not accurately

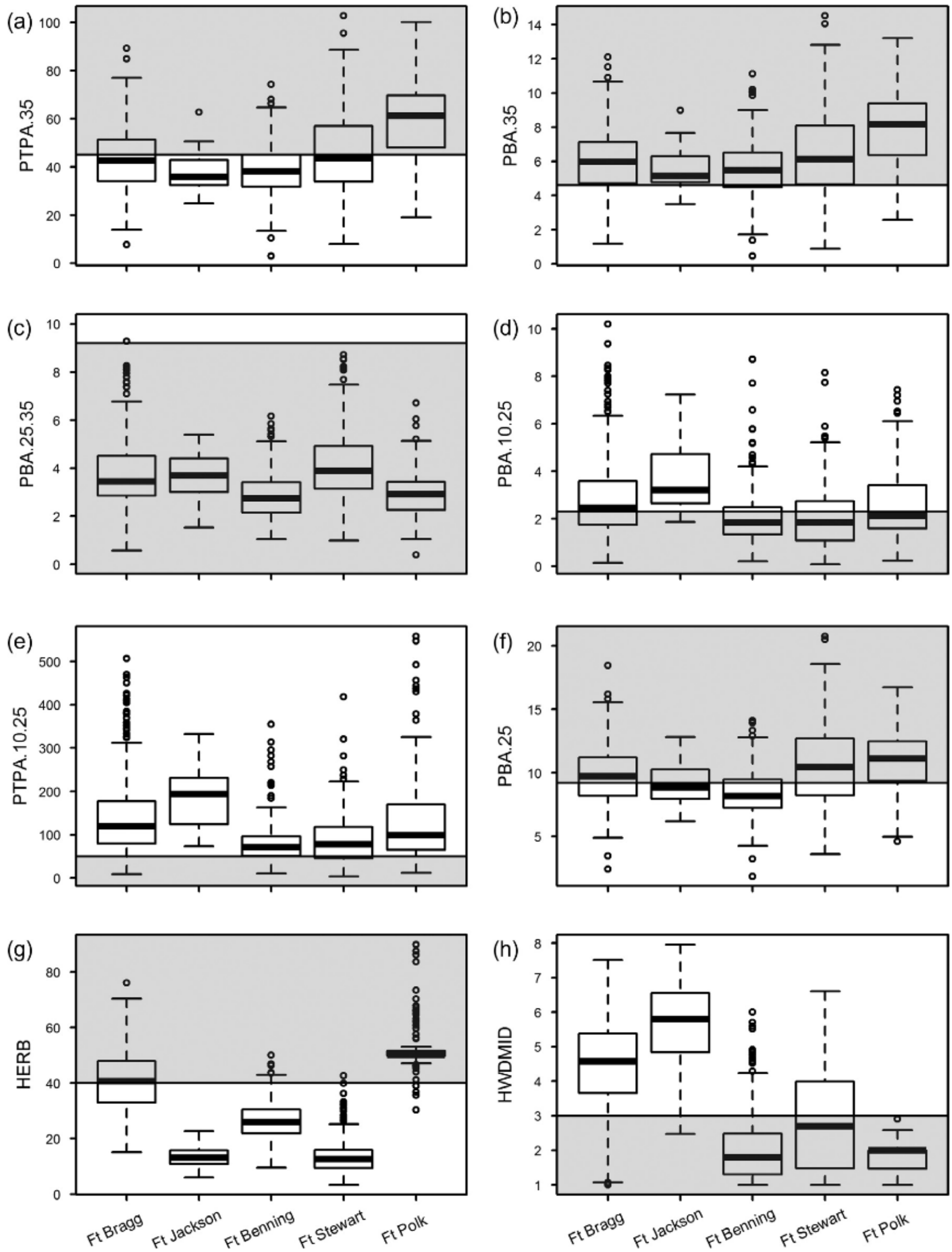

Fig. 3. Variation in eight foraging habitat metrics used to define good quality foraging habitat for the red-cockaded woodpecker (Table 2; USFWS, 2003). Shown are the median, interquartile range and outliers for habitat metrics on territories at each of five military installations. Shaded areas indicate the range of values considered good quality foraging habitat according to the Recovery Plan guidelines. See Table 2 for variable descriptions and units.

represent precise territorial boundaries used by foraging woodpeckers in each region.

Also, we found RCW Matrix Application scores to be very low, indicating that much habitat may be far from high quality despite management efforts. In other words, relationships between model scores and components of bird fitness might have been stronger if more good-quality habitat had been present on the landscape. For example, perhaps too much focus has been placed on hardwood management, when we found little evidence for negative effects of hardwoods (see below). Recent research indicates that negative effects of a dense hardwood midstory operate through groundcover suppression, that a substantial midstory layer can suppress

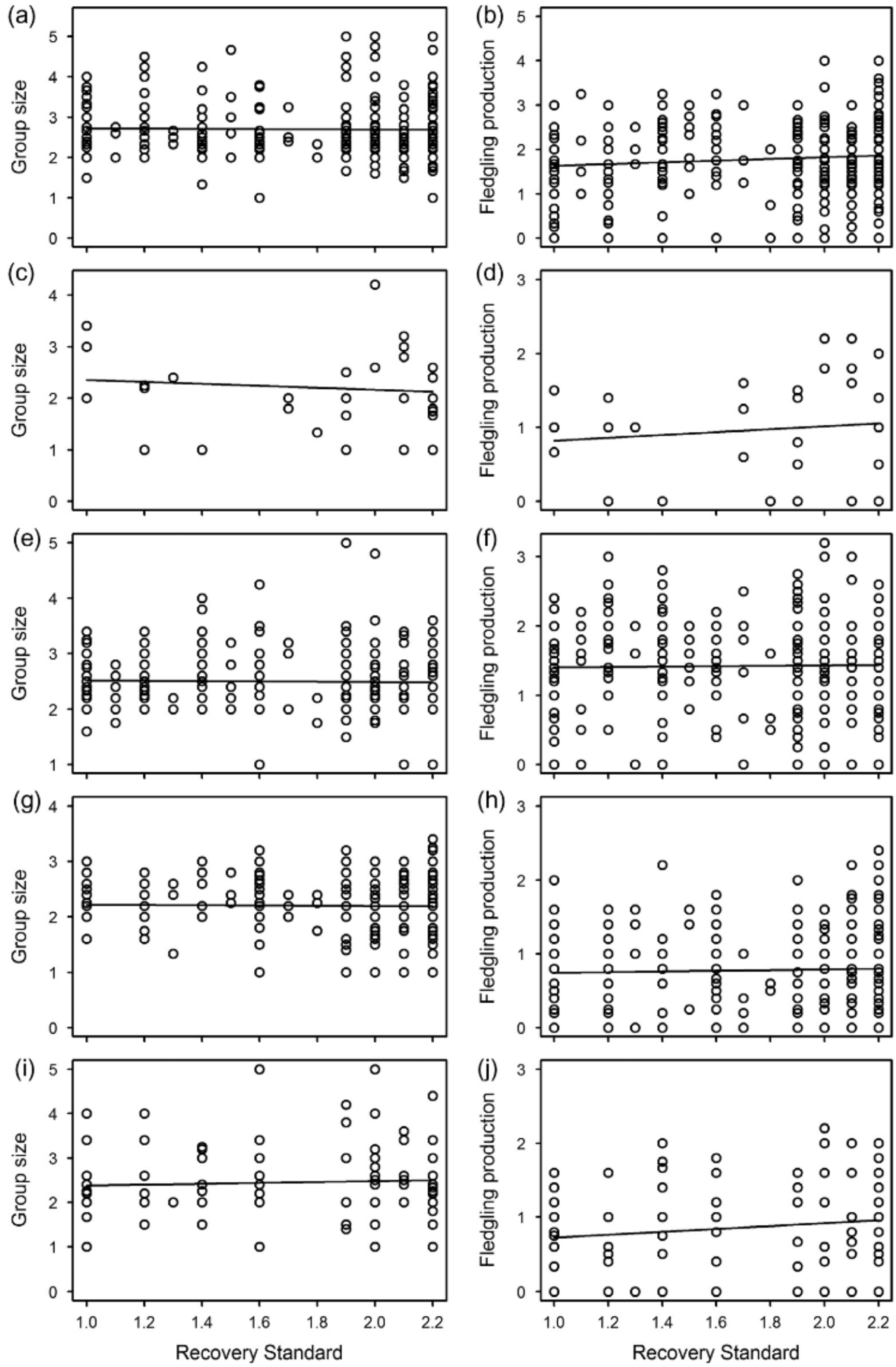

Fig. 4. Relationship between mean group size or fledgling production on territories and Recovery Standard score, as assessed by the RCW Foraging Matrix Application for individual territories at five military installations: (a and b) Fort Bragg, (c and d) Fort Jackson, (e and f) Fort Benning, (g and h) Fort Stewart, (i and j) Fort Polk. Higher scores represent higher-quality foraging habitat, as assessed by the RCW Matrix Application.

groundcover, and that past correlations between hardwood midstory and red-cockaded woodpeckers were difficult to separate from effects of suppressed fires (Hiers et al., 2007). On a related note, certain forest stands and territories may have truly been high-quality habitat, but were overly penalized by the RCW Matrix Application model for their hardwood component.

The lack of an association between model scores and fitness components could result from other factors not addressed by the model. Much of the research that went into developing current foraging habitat guidelines was based primarily on detailed studies at a handful of key sites with fire-maintained restored habitats, including Fort Bragg, NC, and Apalachicola National Forest, FL

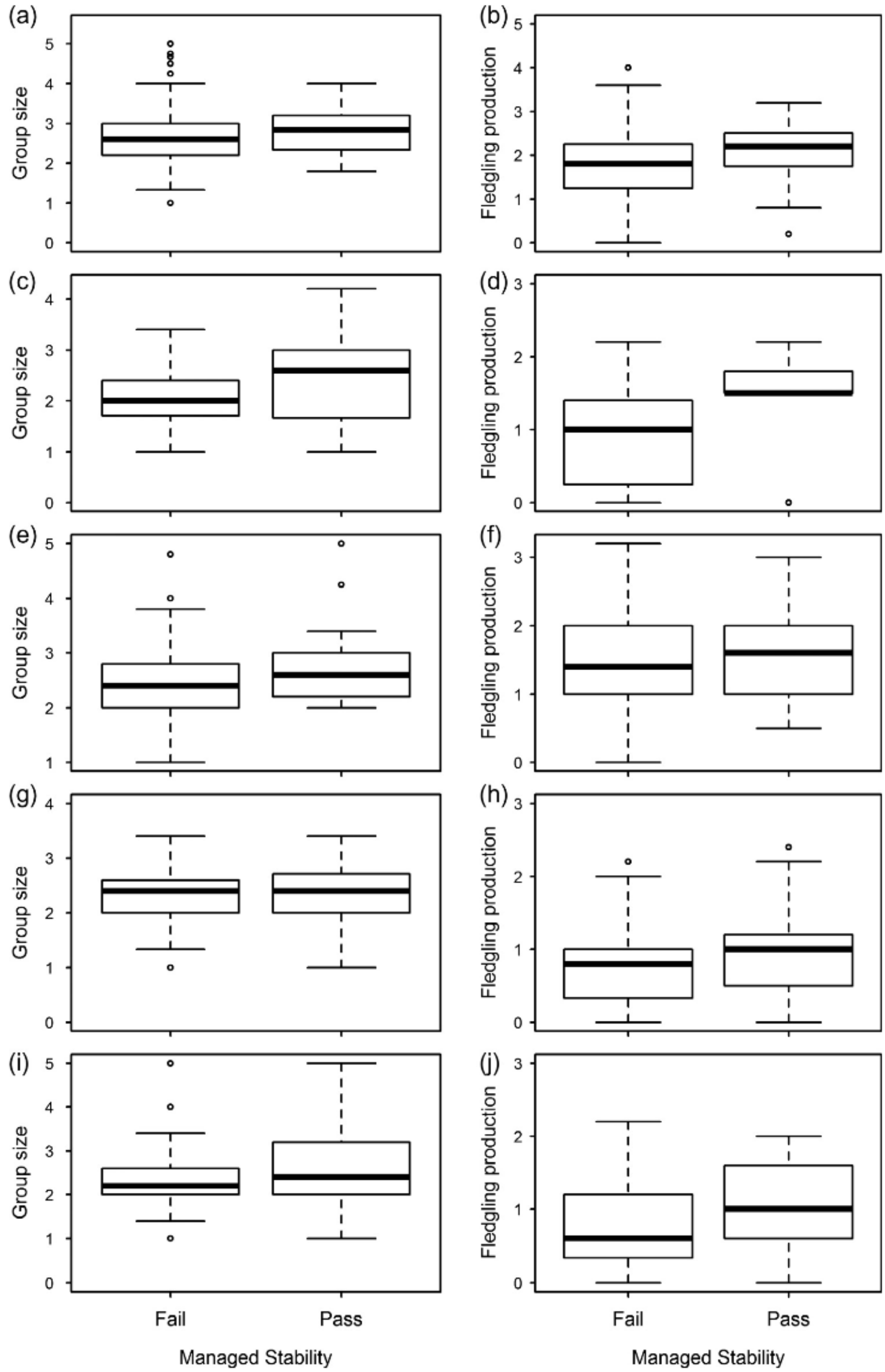

Fig. 5. Distribution of group size or fledgling production on territories with a score of Fail or Pass for Managed Stability, as assessed by the RCW Foraging Matrix Application at five military installations: (a and b) Fort Bragg, (c and d) Fort Jackson, (e and f) Fort Benning, (g and h) Fort Stewart, (i and j) Fort Polk.

(James et al., 1997, 2001; Walters et al., 2002). Those guidelines are now being applied across the range, however, and our range-wide results indicated that generalized models may not accurately reflect relationships between birds and their environments at individual sites. Indeed, Fort Bragg showed some of the few statistically significant associations between habitat scores and fitness components (Fig. 4 and 5), whereas more distant sites did not yield such relationships. Comparisons of group size and fledgling production across all 10 sites revealed range-wide variation in these fitness components (Fig. 2), which indicates potential differences in life-history strategies (Conner et al., 2001). Associations between model scores and red-cockaded woodpecker group size or fledgling production could also be influenced by other environmental factors, such as weather, availability of cavity trees, number

Table 3
Summary of regression tree splits for the relationship between red-cockaded woodpecker group size or fledgling production, and habitat metrics at five military installations. For each site and for models with either group size (group) or fledgling production (fledglings) 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 parentheses. Split value inequalities (< or ⩾) show the direction that leads to larger group size or fledgling production. Also shown in black is the mean ± standard deviation for each habitat metric at each site.

Site		Large pines		Medium pines		Small pines		Large hardwoods		Medium hardwoods		Small hardwoods			
		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	Group	⩾7.5	⩾50.2		(⩾50.4)	2.9 ± 1.6	<297.7								
	Fledglings									⩾0.5	⩾5.2				⩾59.2
	x̄ ± SD	6.0 ± 1.9	43.4 ± 13.0	3.8 ± 1.3	51.8 ± 18.8		142.7 ± 88.4	0.7 ± 0.7	4.3 ± 4.5	0.7 ± 0.5	9.4 ± 7.7	1.5 ± 0.9	92.5 ± 62.3	4.4 ± 1.4	40.7 ± 11.2
Fort Jackson	Group					<2.6	≤174.2							(<4.82)	⩾14.3
	Fledglings	5.3 ± 1.6	36.1 ± 10.5	3.4 ± 1.0	48.5 ± 14.7	<2.6	<174.2, (<174.2)	1.1 ± 1.1	7.3 ± 7.0	1.2 ± 0.3	17.2 ± 4.6	2.4 ± 0.3	132.1 ± 13.2	5.8 ± 1.4	⩾15.3
	x̄ ± SD					3.5 ± 1.2	175.5 ± 48.1								13.4 ± 6.4
Fort Benning	Group	⩾5.5	⩾44.7			<1.62.1 ± 1.5	81.0 ± 78.2	0.5 ± 0.4	3.6±2.5	0.4 ± 0.9	7.0 ± 13.2	0.5 ± 1.3	19.5 ± 79.4	2.0 ± 1.0	⩾27.4, (⩾27.2)
	Fledglings	⩾3.1	⩾24.2												
	x̄ ± SD	5.5 ± 1.5	38.7 ± 9.9	2.9 ± 1.0	43.6 ± 15.6										26.5 ± 5.9
Fort Stewart	Group	≤9.2				⩾0.4, (⩾0.4)	⩾17.4								
	Fledglings	(⩾8.2)		⩾6.7	⩾93.5										⩾14.40
	x̄ ± SD	6.5 ± 2.4	45.8 ± 16.4	4.1 ± 1.4	46.2 ± 19.6	2.1 ± 1.3	88.7 ± 56.4	0.7 ± 0.7	4.3 ± 4.1	0.7 ± 0.5	10.6 ± 7.8	1.3 ± 0.9	15.2 ± 52.6	2.8 ± 1.4	13.4 ± 6.0
Fort Polk	Group	(<9.3)				≤2.0	≤95.9						⩾34.4		
	Fledglings					≤2.3	≤111.1						<8.4		
	x̄ ± SD	8.0 ± 2.2	59.5 ± 16.8	2.9 ± 1.1	46.7 ± 17.9	2.7 ± 1.6	143.0 ± 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

of helpers, and age of breeders (Lennartz et al., 1987; Neal et al., 1993; Walters, 1990). Separating the effects of habitat from these factors, especially from cavity availability, is challenging. Thus, even if foraging habitat were perfectly linked to fitness, breaking down complex and potentially interacting habitat components into a single score is unlikely to fully capture the quality of foraging habitat. Some variables, such as ground cover and large pines, are likely more closely tied to fitness than others, and combining them with other variables of less importance in a single score may dilute fitness correlates.

Localized features may also influence woodpecker group size and fledgling production. Indeed, over the last decade, the use of fire has become widespread and many restored red-cockaded woodpecker habitats differ greatly in attributes such as pine density, hardwood density, and ground cover condition. Red-cockaded woodpeckers can occupy a diversity of habitats that no doubt underlie the species' fundamental niche, although determining whether the fundamental niche itself varies geographically would require manipulative experiments (James et al., 1984). Nonetheless, our regression tree analyses revealed natural break-points in local habitat metrics that were associated with higher or lower fitness components (Table 3). In accordance with current understanding of red-cockaded woodpecker foraging habitat quality, greater basal area and numbers of large pines (>35 cm dbh), greater herbaceous groundcover, and lower basal area and numbers of small pines (10.2–25.4 cm dbh) were frequently identified as important for woodpecker fitness (Table 3). In contrast, results indicating negative effects of hardwoods and medium pines (25.4–35 cm dbh) were rarely seen. We conclude that the RCW Matrix Application captures the habitat features important to fitness, but it also includes features that are no longer important on current landscapes, and for those features that are important the critical threshold values vary among locations.

4.1. Local and regional guidelines

By examining the ranges of threshold values that were associated with woodpecker fitness components, we identified several recommendations for how "global" foraging habitat guidelines might be revised, so as to accommodate the range of habitat conditions that may represent high-quality foraging habitat (McKellar et al., 2013). First, we found that thresholds in percent 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 – for instance, mean herbaceous groundcover at Fort Jackson was 13.4%, and territories with >14.3% were associated with larger groups, whereas mean herbaceous groundcover at Fort Benning was 27.4%, and territories with >26.5% were associated with larger groups (Table 3). Additionally, the 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. 3g). Our results reinforce previous assertions that herbaceous groundcover is a critical attribute of foraging habitat quality, that greater herbaceous content is better up to some threshold, and that many locations such as Fort Jackson and Fort Benning are still well below that threshold. The 40% figure adopted in the Recovery Plan still appears to be an appropriate target, although the data from Fort Bragg indicate that a higher threshold may be appropriate at some locations, and it remains to be seen whether a lower threshold is appropriate for locations such as Fort Jackson and Fort Benning. A promising approach might be to adjust the

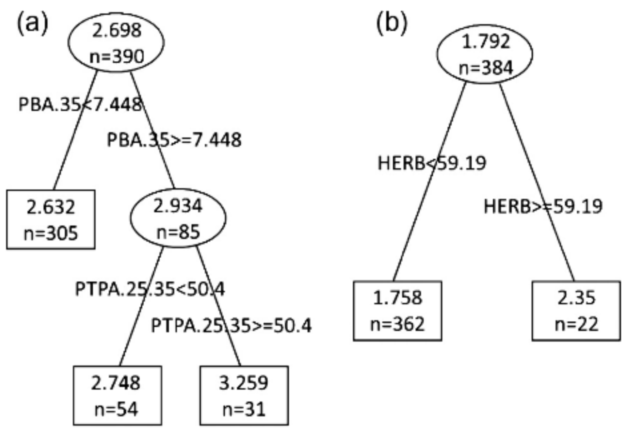

Fig. 6. Sample of a pruned regression tree for evaluating the relationship between (a) group size and (b) fledgling production and 14 habitat metrics at Fort Bragg, NC. Each node is labeled with the mean group size or fledgling production (above) and number of territories (below) falling into that category. 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.

threshold value according to key factors known to affect ground cover composition, namely soil type (Carr et al., 2010) and site productivity. Information about these factors is universally available, and their relationship to groundcover thresholds could easily be explored.

Second, large pine densities above 50.2 and 44.7 stems/ha were associated with larger groups at Fort Bragg and Fort Benning, respectively. Similarly, large pine basal areas of 7.45 and 5.48 m^2/ha 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 recommended in the Recovery Plan (4.6 m^2/ha and 45 stems/ha; Table 2). Our results thus 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; Table 3) at two sites – Fort Stewart and Fort Polk – above which 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 woodpeckers at Fort Bragg decreased with pine (>35.6 cm dbh) densities of more than 90 stems/ha (roughly 9 m^2/ha basal area). Thus, 9.2 m^2/ha basal area and 90 stems/ha 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. Thus it seems possible to identify both lower and upper thresholds for large pines that may apply globally. In this case what should be adjusted according to soil type and local site productivity could be what size is considered “large”. For instance, the size criterion in the Recovery Plan and RCW Matrix Application, i.e., >35 cm dbh, is too large for unproductive sites such as Eglin Air Force Base, Florida (McKellar et al., in preparation).

Third, medium pines were not identified as being among the most important habitat metrics in many of our regression tree analyses, and when they did appear, they showed positive rather than negative effects on group size or reproduction. 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, the vast majority of territories on all sites fell below the recommended maximum for medium pine stocking (Fig. 3c). Positive effects of medium pines were identified at levels far below the recommended maximum in the Recovery Plan (9.2 m^2/ha; Table 2). 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 likely is appropriate but has been rendered irrelevant through forest management on many landscapes. Adjusting pine size criteria to soil type and site productivity as we suggest will alter the definition of medium and well as large pine sizes. It will be necessary to revisit relationships of RCW fitness components to medium pines to determine whether the positive effects we observed relate to (redefined) large or medium size classes of pines.

Fourth, we identified both upper and lower thresholds for small pine basal area and density. Very few sites were below the recommended maximum of 2.3 m^2/ha basal area with fewer than 50 stems/ha of small pines (Fig. 3d and e). Thresholds for negative effects of small pines on group size and/or productivity that were similar to the basal area criterion were identified at three sites (Fort Jackson, Fort Benning, and Fort Polk; Table 3), supporting the use of this metric. In contrast, thresholds for negative effects of numbers of small pines that emerged from our analyses were markedly higher than the Recovery Plan standard (ranging from ~96 to 298 stems/ha). The discrepancy is likely due to the presence of large numbers of very small pine stems on many landscapes. Given that negative effects of small pines arise from development of a midstory layer and not the number of stems per se, 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. We also observed lower thresholds for basal area (0.42 m^2/ha) and number of stems/ha (17.4 stems/ha) associated with larger groups at Fort Stewart. We suspect that these reflect effects of fire history rather than a direct response to small pines.

Fifth, basal area and numbers of hardwoods were found to be associated with fitness components at only two sites (Fort Bragg and Fort Polk), and in three of four cases regression tree splits indicated positive rather than negative effects of higher basal area or numbers of hardwoods (Table 3). Interestingly, the site for which a negative effect of hardwood midstory index was identified, Fort Jackson, had the highest mean hardwood midstory index (Fig. 3h) of the sites assessed herein. Results thus suggest that woodpeckers at Fort Jackson may continue to be impacted by dense hardwood midstory, but that other sites are below this threshold. Taken together, our results indicate 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 (see also Hiers et al., 2014). 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.

We note that the thresholds we identify here vary in how they should be applied. The small pine and hardwood thresholds are limits that should not be exceeded, but do not represent negative habitat factors in that managing for minimum values below the thresholds provides no further benefits and may actually be detrimental. The large pine thresholds provide an optimum range of densities, although site-specific adjustments to the size criterion that account for differences in soil type and site productivity will need to be made. Finally, the groundcover threshold, with appropriate adjustments for soil type and site productivity, likely will represent the metric on which management is most focused as progress toward that threshold represents increased benefit to red-cockaded woodpeckers, and maintaining habitat above that threshold will require continued management action.

4.2. Models in conservation

Results generally aligned with the documented habitat-fitness associations of red-cockaded woodpeckers and the habitat components considered important in the RCW Foraging Matrix Application model (i.e., large pines, herbaceous groundcover). However, the RCW Matrix Application hardly encompassed the range of habitat values used by red-cockaded woodpeckers, and it did not perform well as a predictor of high-quality foraging habitat across the species geographic distribution. This is perhaps not surprising, as models parameterized with data from one geographic location might not generalize well to other locations (McCarthy et al., 2000; Schiegg et al., 2005), particularly when there is considerable geographic variation in habitat structure as in red-cockaded woodpeckers. Other similar examples from the conservation literature include geographic variation in habitat use in northern spotted owls (*Strix occidentalis caurina*; Noon and McKelvey, 1996), and environmental variation in resource selection in ferruginous pygmy owls (*Glaucidium brasilianum*; Flesch and Steidl, 2010). Our results suggest that making site-specific adjustments to parameter values may be an effective way to employ an improved version of the RCW Foraging Matrix Application as a range-wide model.

Modeling approaches in conservation are often based on expert opinion and on limited data, but the utility of those models may be greatly compromised by incomplete data at the time of inception. Our results indicated that much improvement could be made to models by using additional data from restored habitats and updated analysis techniques, and that further analyses may yield insights into whether single models are accurate representations of populations at large, or whether more localized approaches are necessary. Specifically, we believe that within the context of increasingly restored landscapes, the RCW Matrix Application may place too much emphasis on hardwood midstory, when recent research indicates that fire alone may be sufficient to an appropriate presence of hardwoods (Steen et al., 2013). The lack of a strong association between model scores and components of woodpecker fitness suggests that an adequate amount of high-quality habitat is lacking and/or a more accurate, current representation of good-quality habitat is needed. Conservation models have become central to planning and management, especially in light of changing climates (Carroll, 2010), but validating and revising models will remain crucial if they are to be useful for conservation and decision-making.

4.3. Management implications

The red-cockaded woodpecker was among the first species listed as endangered in the U.S. Endangered Species Act of 1973 (U.S. Code Title 16, Chapter 35, Section 1531–1544), and since then much effort has been invested in population recovery. Current foraging habitat guidelines (USFWS, 2003) include recommended thresholds of habitat conditions that are applied at the range-wide scale (Table 2). However, our results indicate that attempting to define high-quality habitat based on a “one-size-fits-all” model developed with few examples ignores important geographic variation in habitat structure, and may set unrealistic management goals in regions incapable of reproducing the ideal habitat. In this way, our site-specific findings are directly applicable to managers attempting to increase local red-cockaded woodpecker productivity (McKellar et al., 2013). Our results also highlight current “global” foraging habitat guideline features that could potentially be eased or adjusted so as to accommodate the range of habitat conditions acceptable to red-cockaded woodpeckers. Overall, we argue that large pines and herbaceous groundcover remain crucial components of high-quality foraging habitat for red-cockaded woodpeckers, but that current recommended values for hardwoods and small pines may be overly stringent.

Acknowledgments

We thank the many members of the Department of Defense and Department of Agriculture National Forests who shared their data and facilitated data transfer to the University of Missouri, including M. Barron, J. Britcher, L. Carlile, S. Carnahan, J. Drake, R. Fleming, J. Gainey, M. Garner, C. Garrett, N. Hawkins, D. Heins, E. Hoffman, S. Hudson, J. Maitland, S. Marcantel, T. Marston, C. Medler, W. Montague, K. Moore, D. Morrow, S. Pulsifer, T.J. Quarles, K. Rutkofske, and J. Schillaci. T. Hayden, R. Kirgan, W. McDearman, and M. Trager provided valuable discussion and feedback on earlier drafts. We thank J. Carter, P. Doerr, the Sandhills Ecological Institute and the many staff, graduate students and field assistants from Virginia Tech and North Carolina State University who have contributed to collection of demographic data at Fort Bragg. We appreciate the helpful comments on early manuscript drafts provided by F. James and an anonymous reviewer. Funding was provided through a cooperative agreement between the Engineer Research and Development Center – Construction and Engineering Research Laboratory (ERDC – CERL) and the University of Missouri. This work was sponsored by the Department of Defense; the content of the information does not necessarily reflect the position or the policy of the government, and no official endorsement should be inferred.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.04.007.

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