Systematic Review of the Influence of Foraging Habitat on Red-Cockaded Woodpecker Reproductive Success

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Source: Wildlife Biology, 20(1) : 37-46

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.13004

Wildlife Biology 20: 37–46, 2014
doi: 10.2981/wlb.13004

Subject Editor: Ilse Storch. Accepted 27 September 2013

Systematic review of the influence of foraging habitat on red-cockaded woodpecker reproductive success

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Relationships between foraging habitat and reproductive success provide compelling evidence of the contribution of specific vegetative features to foraging habitat quality, a potentially limiting factor for many animal populations. For example, foraging habitat quality likely will gain importance in the recovery of the threatened red-cockaded woodpecker *Picoides borealis* (RCW) in the USA as immediate nesting constraints are mitigated. Several researchers have characterized resource selection by foraging RCWs, but emerging research linking reproductive success (e.g. clutch size, nestling and fledgling production, and group size) and foraging habitat features has yet to be synthesized. Therefore, we reviewed peer-refereed scientific literature and technical resources (e.g. books, symposia proceedings, and technical reports) that examined RCW foraging ecology, foraging habitat, or demography to evaluate evidence for effects of the key foraging habitat features described in the species' recovery plan on group reproductive success. Fitness-based habitat models suggest foraging habitat with low to intermediate pine *Pinus* spp. densities, presence of large and old pines, minimal midstory development, and herbaceous groundcover support more productive RCW groups. However, the relationships between some foraging habitat features and RCW reproductive success are not well supported by empirical data. In addition, few regression models account for $>30\%$ of variation in reproductive success, and unstandardized multiple and simple linear regression coefficient estimates typically range from -0.100 to 0.100, suggesting ancillary variables and perhaps indirect mechanisms influence reproductive success. These findings suggest additional research is needed to address uncertainty in relationships between foraging habitat features and RCW reproductive success and in the mechanisms underlying those relationships.

The relationships between reproductive success and habitat characteristics represent a fundamental challenge in ecology (Fretwell and Lucas 1970, Morris 1987, Clark and Shutler 1999). Patterns in these relationships provide strong evidence that specific habitat features are important components of habitat quality and thus facilitate effective management of animal populations (Walters et al. 2002). Assessment of these relationships is particularly important for threatened species (Foin et al. 1998).

The red-cockaded woodpecker *Picoides borealis* (RCW) is endemic to pine *Pinus* spp. forests of the southern USA and it is listed as federally endangered (US Fish and Wildlife Service 1970). Habitat loss, particularly longleaf pine *P. palustris* forests and old pines required for nesting and roosting, was the primary historic cause of the species' decline (Ligon et al. 1986, Conner and Rudolph 1989, Walters et al. 2002). The effects of habitat loss (Conner and O'Halloran 1987, Rudolph and Conner 1991, Walters et al. 2002) and fire suppression (Conner and Rudolph 1989, Costa and Escano 1989) have been well studied in regard to nesting habitat (i.e. the cavity tree cluster and area within approximately 61 m of the cluster), which has been considered the foremost limiting factor for RCW populations (Walters et al. 1992, 2002). As nesting constraints are now mitigated through techniques such as prescribed burning and artificial cavity construction (Copeyon 1990, Allen 1991), foraging habitat (i.e. area within 0.8 km of the cluster) management likely will gain importance in the recovery of this species (Walters et al. 2002, US Fish and Wildlife Service 2003).

The first revision of the RCW recovery plan highlighted the need to describe foraging habitat requirements (US Fish and Wildlife Service 1985). Guidelines for management of RCW foraging habitat outlined in this revision (hereafter, revised foraging habitat guidelines) were based on resource selection studies in coastal South Carolina, USA (Hooper and Lennartz 1981, Hooper and Harlow 1986). The revised foraging habitat guidelines recommended each RCW group (i.e. the breeding pair and associated helpers if present) have access to ≥ 51 ha of foraging habitat with

40% of the trees at ≥60 year old, ≥6350 pines ≥25.4 cm dbh, and 789.8 m^2 basal area (BA) of pines ≥10.2 cm dbh within an 800 m radius of the cluster. Although these guidelines are unrealistically precise, they provided targets for creating foraging habitat conditions. However, a standard for RCW foraging habitat quality also should reference demography, as such a standard ideally should be supported by information describing both resource selection and reproductive success (Van Horne 1983, Walters et al. 2002).

Researchers were unable to establish reliable relationships between the revised foraging habitat guidelines and RCW reproductive success (e.g. clutch size, fledgling production, group size and nestling production; Beyer et al. 1996, Wigley et al. 1999, James et al. 2001, Walters et al. 2002). Even in the same RCW population on which the revised foraging habitat guidelines were based, group reproductive success did not change after timber harvests reduced mean number of pines ≥25.4 cm dbh per group to 60% below recommended levels (Hooper and Lennartz 1995). The weak associations between the revised foraging habitat guidelines and RCW reproductive success suggest that either: 1) reduction of foraging habitat has limited influence on reproductive success; 2) the revised foraging habitat guidelines provide inappropriate standards; or 3) the effects of foraging habitat features on group reproductive success are variable depending on other foraging habitat features (Beyer et al. 1996, James et al. 2001, Walters et al. 2002).

Additional research on RCW foraging ecology and demography refined the standard of quality foraging habitat. Researchers documented positive relationships between RCW group reproductive success and open foraging habitat with low to intermediate pine densities, some large and old pines, intermittent midstory trees and shrubs, and abundant herbaceous groundcover (Hardesty et al. 1997, James et al. 1997, 2001, Convery 2002, Walters et al. 2002). Therefore, foraging habitat guidelines were further revised in the species' current, i.e. 2003, recovery plan to reflect these relationships (US Fish and Wildlife Service 2003). Key features of good quality foraging habitat in the 2003 guidelines included: 1) substantial herbaceous groundcover, 2) minimal hardwood midstory, 3) minimal pine midstory, 4) minimal hardwood overstory, 5) low to intermediate density of small and medium pines, and 6) a significant presence of large and old pines.

Despite the central role of foraging habitat quality in the 2003 recovery plan, relationships between key features of the current foraging habitat guidelines and group reproductive success have not been thoroughly reviewed. Periodic evaluation of the empirical data and mechanisms supporting the relationships between the 2003 foraging habitat guidelines and RCW reproductive success has been lacking, but represents a critical exercise to ensure the guidelines are an appropriate standard for foraging habitat management. To examine relationships between foraging habitat features described in the species' recovery plan and group reproductive success, we systematically reviewed studies of RCW foraging ecology and demographics. Our primary objectives were to: 1) present a review of research describing relationships between key foraging habitat features and RCW reproductive success, 2) describe potential mechanisms that drive relationships between key foraging habitat features and RCW reproductive success, and 3) evaluate the degree of empirical support for relationships between key foraging habitat features and reproductive success.

Material and methods

We searched online databases (BioOne, JSTOR, Wildlife and Ecology Studies Worldwide, ScienceDirect, Searchable Ornithological Research Archive) and used the internet search engine Google Scholar (<www.scholar.google.com>) to compile peer-reviewed scientific literature and technical resources (e.g. books, symposia proceedings, and technical reports) that examined the red-cockaded woodpecker *Picoides borealis* (RCW) foraging ecology, foraging habitat, or demography. We searched for RCW literature containing the key words or phrases, 'demography', 'fitness', 'foraging behavior', 'foraging ecology', 'foraging habitat', 'prey', 'productivity' or 'reproductive success', and selected resources relevant to our objectives. We considered resources relevant to our objectives if they examined the effects of foraging habitat features on RCW reproductive success, foraging behavior, arthropod prey availability or selection, foraging habitat quality, or resource selection by foraging RCWs. Additionally, we searched reference citations of all resources to identify any studies conducted prior to digital indexing.

We organized the results and discussion of our systematic review around the relationships between key foraging habitat features described by the current foraging habitat guidelines and RCW reproductive success (US Fish and Wildlife Service 2003). We evaluated biological importance of these relationships based on the magnitude of effect sizes alone because precision estimates were not provided in most studies (Cohen 1994, Grafen and Hails 2002, Garamszegi et al. 2009). The paucity of reported effect sizes precluded a formal meta-analysis. We included effect size statistics and associated precision estimates when they were reported because these data tend to be more informative than statistical significance (Anderson et al. 2001, Vetter et al. 2013). Effect size statistics reported in the literature included unstandardized multiple and simple linear regression coefficients, Pearson product moment correlation coefficients, unstandardized logistic regression coefficients, and discriminant function coefficients.

We did not compare effect size statistics directly among studies due to varying or ambiguous definitions of foraging habitat metrics (e.g. definitions of old-growth pines), varying scales of explanatory variables (pines/ha averaged by stand or the number of ha in which a threshold level of pines/ha was satisfied), varying sample sizes that potentially biased effect size estimates and inconsistent reporting of effect size precision estimates. Further, effect size statistics documented in correlative studies may be confounded by unmeasured variables and thus are not as definitive as those from manipulative experiments (Johnson 2002). We did not systematically interpret the biological importance of effect size statistics on a priori decision rules (e.g. benchmarks for small, medium, and large effect size statistics), as translating effect size statistics into biological importance based on decision rules is context-dependent (e.g. the magnitude of regression coefficients depends on units of measurement, which varied among studies) and subject to criticisms analogous to the use of arbitrary p-values (Thompson 2001, Nakagawa and Cuthill 2007).

Results

We reviewed 147 publications spanning 1968 to 2010 that examined the red-cockaded woodpecker *Picoides borealis* (RCW) foraging ecology or foraging habitat or linked habitat to demography. Eleven studies explicitly examined the relationship between RCW foraging habitat and group reproductive success (Table 1). We identified no study in a refereed journal that explicitly examined RCW reproductive success in response to the 2003 foraging habitat guidelines. Seven of the 11 studies that directly examined RCW group reproductive success in response to foraging habitat features provided estimates of effect size statistics; two provided precision estimates (Table 1). The number of habitat variables measured by researchers that explicitly examined RCW foraging habitat-reproductive success relationships averaged 14.7 (SE = 3.28, n = 11) but ranged from 5 to 36 (Table 1). Sample sizes averaged 47.9 (SE = 8.92, n = 11) and ranged from 20 to 99 RCW groups (Table 1). Measures of reproductive success included clutch size, nestling and fledgling production, group size and a composite measure of reproductive success derived from a combination of reproductive success metrics. The most common extent at which foraging habitat characteristics were measured was 200 ha (equivalent to a circular 800-m foraging partition; Table 1). Pairwise correlations or variance inflation factors of explanatory variables were not reported in any study. Researchers either reported the absence of significant collinearity (e.g. $r \geq 0.70$) among explanatory variables included in statistical models or omitted one of the two correlated variables from subsequent analyses.

Linear regression was the most common method for assessing relationships between RCW reproductive success and foraging habitat features (Table 1). Four of the seven studies that used linear regression reported regression coefficient estimates; one provided precision estimates (Table 1). Reported coefficients of all explanatory variables included in multiple and simple linear regression models ranged from −0.705 to 0.278; of the 57 reported coefficients, 43 ranged from −0.100 to 0.100 (Table 2). Partial coefficients of determination for explanatory variables included in multiple linear regression models were not reported in any study. Variation in RCW reproductive success metrics accounted for by reported multiple and simple linear r egression models (R^2 and adj. R^2) ranged from 0% to 60% (Table 2).

Table 1. A synopsis of studies that directly examined the relationships between red-cockaded woodpecker (RCW) reproductive success metrics and foraging habitat features in the southeastern USA. Presented data include the study location, type(s) of analyses used to examine the relationship between RCW reproductive success and foraging habitat, number of foraging habitat variables measured (explanatory variables), the extent at which foraging habitat variables were measured around clusters, sample size of RCW groups, the reproductive success metric analyzed (response), if effect parameter effect size statistics were reported (effect size), and if precision estimates of parameter effect sizes were reported (precision estimates).

Study	Location	Analyses	Explanatory variables[a]	Extent	Sample size	Response[b]	Effect size	Precision estimates[c]
Hooper and Lennartz 1995	South Carolina	*t*–test	5	607 ha	24	C, N, F, G	no[d]	no
Beyer et al. 1996	Florida	linear regression, Kruskal–Wallis, ANOVA	7	200 ha	60	F, G	no	no
Hardesty et al. 1997	Florida	linear regression	35	home-range	25	C, N, F, G	yes	no
James et al. 1997	Florida	linear regression, Pearson correlation	10	200 ha	87	C, F, G	yes	no
Wigley et al. 1999	Louisiana	logistic regression, Mann–Whitney	36	200 ha	22–24	C, F	yes	yes
Davenport et al. 2000	North Carolina	discriminant function	19	200 ha	99	FIT	yes[e]	no[f]
James et al. 2001	Florida	linear regression, Pearson correlation	18	200 ha, core stands[g]	47–55	G	yes	no
Convery 2002	North Carolina	linear regression	8	200 ha, home-range	23	G, F	yes	yes
Walters et al. 2002	North Carolina	linear regression	9	home-range	30	G	no	no
Spadgenske et al. 2004	Georgia	ANOVA, linear regression	8	200 ha	80	C, F	no	no
Butler and Tappe 2008	Arkansas, Louisiana	*t*–test, Pearson correlation	14	foraging sites[h]	10–20	C, N, F	yes	no

[a]includes all covariates measured in the study regardless of inclusion in statistical models.
[b]C = clutch size, N = nestling production, F = fledgling production, G = group size, FIT = a composite ranking variable derived from a function based on weighted values for 1) number of helpers, 2) number of fledglings, 3) group size, and 4) number of breeders.
[c]confidence intervals or standard errors of effect size estimates.
[d]includes Cohen's *d* (Cohen 1992).
[e]unknown if coefficients were reported as unstandardized, standardized, or structure coefficients.
[f]includes tolerance intervals.
[g]core stands include habitat of the cluster site and surrounding areas with fairly homogeneous habitat structure.
[h]foraging sites represented a group's foraging location during fixed-interval time point sampling efforts.

Table 2. Reported linear regression statistics modeling foraging habitat parameters and red-cockaded woodpecker mean clutch size (Clutch), fledgling production (Fledgling), group size (Group), and nestling production (Nestling) in the southeastern United States.

Measure	Model statistics K[a]	$R^{2,b}$	p > F	Parameters	p > *t*	Effect size[c]	SE
Clutch							
Hardesty et al. 1997	1	0.28	0.009	mean hardwood height (m)		−0.705	
	1	0.26	0.013	mean hardwood dbh (cm)		−0.359	
	1	0.25	0.012	% forb groundcover		0.003	
	1	0.24	0.014	% pine litter groundcover		−0.001	
	1	0.24	0.014	pines ≥ 25.4 cm dbh ha^{-1}		−0.078	
James et al. 1997	1	0.08	0.008	% wiregrass *Aristida stricta* groundcover		0.020	
	2	0.08	0.022	% wiregrass groundcover		0.010	
				% saw palmetto *Serenoa repens* groundcover		−0.010	
Spadgenske et al. 2004	5	0.17	0.04	pines ≥ 35.6 cm dbh ha^{-1}			
				pines ≤ 25.4 cm dbh ha^{-1}			
				BA of pines 25.4–35.6 cm dbh (m^2 ha^{-1})			
				% herbaceous groundcover			
				BA of hardwoods (m^2 ha^{-1})			
	5	0.12	0.39	ha with ≥ 45 pines ≥ 35.6 cm dbh			
				ha with < 50 pines ≤ 25.4 cm dbh			
				ha with BA of pines 25.4–35.6 cm dbh ≤ 9.2 (m^2 ha^{-1})			
				ha with ≥ 40% herbaceous groundcover			
				ha with BA of hardwoods < 2.3 (m^2 ha^{-1})			
	1	0.07	0.030	ha with ≥ 45 pines ≥ 35.6 cm dbh			
	1	0.00	0.77	ha with < 50 pines ≤ 25.4 cm dbh			
	1	0.06	0.040	ha with BA of pines 25.4–35.6 cm dbh ≤ 9.2 (m^2 ha^{-1})			
	1	0.03	0.19	ha with ≥ 40% herbaceous groundcover			
	1	0.00	0.84	ha with BA of hardwoods < 2.3 (m^2 ha^{-1})			
	1	0.05	0.07	ha with BA of pines ≥ 35.6 cm dbh ≥ 4.6 (m^2 ha^{-1})			
	1	0.00	0.77	ha with BA of pines ≤ 25.4 cm dbh ≤ 2.3 (m^2 ha^{-1})			
	1	0.07	0.04	ha with BA of pines ≥ 25.4 cm dbh ≥ 9.2 (m^2 ha^{-1})			
Fledgling							
Beyer et al. 1996	1	0.04	0.002	no. active clusters within 2 km of cluster	0.005		
	1	0.04	0.060	no. pines > 25.4 cm dbh within 400 m of cluster	0.49		
	1	0.03	0.070	no. pines > 25.4 cm dbh within 800 m of cluster	0.71		
	1	0.03	0.030	ha of foraging habitat within 400 m of cluster	0.19		
	1	0.02	0.070	ha of foraging habitat within 800 m of cluster	0.71		
	1	0.02	0.060	% non-foraging habitat within 800 m of cluster	0.39		
	1	0.02	0.040	angular sum	0.23		
Hardesty et al. 1997	1	0.35	0.002	% forb groundcover		0.003	
	1	0.30	0.005	pines ≥ 25.4 cm dbh ha^{-1}		−0.061	
	1	0.24	0.012	BA of pines > 30.5 cm dbh (m^2 ha^{-1})			
	1	0.22	0.017	% pine litter groundcover		−0.001	
	1	0.19	0.029	Mean pine dbh (cm)		−0.107	
	1	0.19	0.028	BA of total pines (m^2 ha^{-1})		−0.155	
	1	0.17	0.037	BA of live pines (m^2 ha^{-1})		−0.151	
	1	0.17	0.036	mean pine height (m)		−0.155	
James et al. 1997	2	0.13	0.003	% wiregrass groundcover		0.010	
				natural pine regeneration		0.002	
	1	0.08	0.008	natural pine regeneration		0.003	
	1	0.08	0.007	% wiregrass groundcover		0.010	
	1	0.04	0.058	% gallberry *Ilex glabra* groundcover		0.010	
Convery 2002	8	0.54	0.009	home range size	0.001	0.020	0.005
				pines 25.4–35.6 cm dbh ha^{-1}	0.010	−0.019	0.006
				hardwoods ≥ 25.4 cm dbh ha^{-1}	0.016	−0.158	0.057
				unsuitable habitat[d]	0.035	−0.026	0.011
				local population density	0.035	0.231	0.099
				herbaceous groundcover	0.036	0.027	0.012
				pines > 35 cm dbh ha^{-1}	0.047	0.015	0.007
				midstory height (m)	0.075	−0.159	0.083
Spadgenske et al. 2004	5	0.12	0.17	pines ≥ 35.6 cm dbh ha^{-1}			
				pines ≤ 25.4 cm dbh ha^{-1}			
				BA of pines 25.4–35.6 cm dbh (m^2 ha^{-1})			
				% herbaceous groundcover			
				BA of hardwoods (m^2 ha^{-1})			

(Continued)

Table 2. (Continued).

Measure	Model statistics K[a]	$R^{2,b}$	p > F	Parameters	p > t	Effect size[c]	SE
	5	0.12	0.37	ha with ≥ 45 pines ≥ 35.6 cm dbh			
				ha with < 50 pines ≤ 25.4 cm dbh			
				ha with BA of pines 25.4–35.6 cm dbh ≤ 40 (m^2 ha^{-1})			
				ha with ≥ 40% herbaceous groundcover			
				ha with BA of hardwoods < 2.3 (m^2 ha^{-1})			
	1	0.02	0.32	ha with ≥ 45 pines ≥ 35.6 cm dbh			
	1	0.01	0.55	ha with < 50 pines ≤ 25.4 cm dbh			
	1	0.07	0.040	ha with BA of pines 25.4–35.6 cm dbh ≤ 40 (m^2 ha^{-1})			
	1	0.01	0.52	ha with ≥ 40% herbaceous groundcover			
	1	0.01	0.52	ha with BA of hardwoods < 2.3 (m^2 ha^{-1})			
	1	0.01	0.38	ha with BA of pines ≥ 35.6 cm dbh ≥ 4.6 (m^2 ha^{-1})			
	1	0.01	0.55	ha with BA of pines ≤ 25.4 dbh ≤ 2.3 (m^2 ha^{-1})			
	1	0.03	0.16	ha with BA of pines ≥ 25.4 cm dbh ≥ 9.2 (m^2 ha^{-1})			
Group							
Hardesty et al. 1997	1	0.17	0.042	% forb groundcover		0.019	
James et al. 1997	2	0.26	< 0.001	% WIRE		0.010	
				% gallberry groundcover		−0.020	
	2	0.24	< 0.001	natural pine regeneration		0.002	
				% gallberry groundcover		−0.020	
	1	0.20	< 0.001	% gallberry groundcover		−0.030	
	1	0.18	< 0.001	% wiregrass groundcover		0.020	
	1	0.13	< 0.001	natural pine regeneration		0.003	
James et al. 2001	3	0.31	< 0.001	large pines[e] ha^{-1} – small pines[f] ha^{-1}		0.002	
				% wiregrass groundcover – % WOPM[g]		0.003	
				no. of relict trees$^{1/2}$		0.070	
	2	0.31	< 0.001	large pines ha^{-1} – small pines ha^{-1}		0.003	
				% wiregrass groundcover – % WOPM		0.003	
	1	0.27	< 0.001	large pines ha^{-1} – small pines ha^{-1}		0.004	
	1	0.26	< 0.001	% wiregrass groundcover – % WOPM		0.005	
	1	0.17	0.003	no. of relict trees$^{1/2}$		0.190	
Convery 2002	7	0.60	0.002	% herbaceous groundcover	0.001	0.044	0.014
				pines 25.4 – 35.6 cm dbh ha^{-1}	0.003	−0.027	0.008
				home range size	0.006	0.020	0.006
				hardwoods < 25.4 cm dbh ha^{-1}	0.014	−0.022	0.079
				local population density	0.030	0.278	0.116
				unsuitable habitat	0.104	−0.017	0.015
				pine age	0.213	0.034	0.029
Walters et al. 2002	3	0.39		flat-tops[h] ha^{-1}	0.003		
				pines 25.4–35.6 cm dbh ha^{-1}	0.020		
				hardwood midstory height (m)	0.070		
Nestling							
Hardesty et al. 1997	1	0.29	0.006	% pine litter groundcover		−0.001	
	1	0.22	0.019	BA of total pines (m^2 ha^{-1})		−0.199	
	1	0.22	0.018	BA of pines ≥ 25.4 cm dbh (m^2 ha^{-1})		−0.063	
	1	0.19	0.039	mean hardwood height (m)		−0.482	
	1	0.19	0.026	% cover of hardwood stems		−0.003	
	1	0.19	0.026	BA of live pines (m^2 ha^{-1})		−0.193	

[a]no. of parameters.
[b]adjusted R^2 is reported for James et al. 1997 and Convery 2002.
[c]unstandardized linear regression coefficients.
[d]unforested areas, pine/pine-hardwood stands < 30 year old, areas dominated by hardwoods, and pine/pine-hardwood stands < 30 year old and average dbh < 17.78 cm.
[e]≥ 35 cm dbh.
[f]15–25 cm dbh.
[g]woody vegetation groundcover + saw palmetto *Serenoa repens* groundcover.
[h]old pines with characteristic growth form.

Understory composition

Current evidence suggests the direct contribution of herbaceous groundcover to RCW group reproductive success is small; multiple and simple linear regression coefficients range from 0.003 to 0.044 and few models account for $>30\%$ of the variation in reproductive success (Table 2). James et al. (1997) reported larger mean clutch sizes during the first breeding season after territories were burned, also implicating herbaceous groundcover as a driver. In contrast, Spadgenske et al. (2004) reported the number of ha compliant with minimum recommended level of herbaceous groundcover ($\geq 40\%$) was not significantly related to clutch size or fledgling production.

Midstory encroachment

Evidence for a relationship between midstory encroachment and RCW reproductive success was mixed. Group size and fledgling production declined as midstory height in foraging habitat increased in two studies (Table 2); the effect size was reported in only one study. Davenport et al. (2000) documented a decline in a composite measure of group reproductive success as mean height of all trees and shrubs above the groundcover increased; the discriminant function coefficient was -0.10. Spadgenske et al. (2004), however, reported the number of ha of RCW foraging habitat with BA of hardwoods <2.3 m^2 ha^{-1}, used as a surrogate for hardwood midstory, was not related to clutch size or fledgling production.

Hardwood overstory

Large hardwood overstory was negatively related to RCW reproductive success, but reported effects were variable (Table 2). Hardesty et al. (1997) reported a decline in clutch size and nestling production as hardwood height in foraging habitat increased. In the same study, nestling production declined as hardwood dbh and percent cover of hardwood stems increased. Convery (2002) reported a decline in fledgling production as the density of hardwoods ≥ 25.4 cm dbh increased. Butler and Tappe (2008) reported a decline in clutch size and nestling production ($r = -0.59$ and $r = -0.33$, respectively) as hardwood dbh increased and a decline in clutch size ($r = -0.36$) as hardwood canopy cover (%) increased.

Pine age and size

Large and old pines (e.g. pines >35 cm dbh and old-growth pines) generally had consistent positive effects on RCW group reproductive success, whereas broadly defined (e.g. pines ≥ 25.4 cm dbh) and medium (e.g. pines 25.4–35.6 cm dbh) pine size classes tended to have negative effects. The discriminant function coefficient of mean pine dbh in RCW foraging habitat reported by Davenport et al. (2000) was -0.47. Effects of the density of pines ≥ 25.4 cm dbh and pines 25.4–35.6 cm dbh were negative, with multiple and simple linear regression coefficients ranging from -0.078 to -0.019 (Table 2). However, Hooper and Lennartz (1995) reported reproductive success of RCW groups was not affected by removal of 43% of pines $\geq$ 25.4 cm dbh in RCW foraging habitat, suggesting the total number of pines ≥ 25.4 cm dbh available to foraging RCWs did not contribute to group reproductive success. Similarly, Wigley et al. (1999) reported foraging habitat features (e.g. number and BA [m^2 ha^{-1}] of pines 10.1–25.4 cm dbh ha^{-1}, number and BA pines ≥ 25.4 cm dbh ha^{-1}) had no effect on the presence of eggs or fledglings. The density of pines $\geq$ 35 cm dbh and old-growth pines had positive multiple and simple linear regression coefficients ranging 0.015 to 0.190 (Table 2). Basal area of pines >30.5 cm dbh had a negative effect on fledgling production in one study, but the magnitude of the effect was not reported (Table 2; Hardesty et al. 1997). Multiple and simple linear regression coefficients of interactions between pine size class densities (i.e. large pines ha^{-1} – small pines ha^{-1}; James et al. 2001) were small, ranging from 0.003 to 0.004 (Table 2).

Discussion

Our review of existing literature indicates the relationships between RCW group reproductive success and many key foraging habitat features described in the species' current recovery plan (US Fish and Wildlife Service 2003) are inconsistent and weak. Parsing effects of individual foraging habitat features to elucidate underlying mechanisms represents a complex process due to the multidimensional framework of habitat features that constitute the current foraging habitat guidelines. Our results highlight the need for further research validating the relationships between the 2003 foraging habitat guidelines and RCW group reproductive success.

Understory composition

The positive effect that herbaceous groundcover may have on red-cockaded woodpecker *Picoides borealis* (RCW) group reproductive success appears to be minimal; multiple and simple linear regression coefficient estimates are small and few models account for large proportions of the variance in reproductive success. Moreover, precision estimates for linear regression coefficients of groundcover variables are seldom reported, increasing uncertainty in the biological effect that groundcover may have on RCW reproductive success or foraging habitat quality. Existence of indirect mechanisms (e.g. movement of arthropods from groundcover to tree boles and increased nutritive value of arthropod prey items in frequently burned habitat; James et al. 1997) relating herbaceous groundcover to RCW reproductive success are not well substantiated in scientific literature. Detritivores and predators, both important in the RCW diet, represent the majority of arthropod biomass on pine boles (Hanula and Horn 2004), and neither group is reliant on herbaceous groundcover. Several stand and tree characteristics may influence the arthropod prey base of RCWs more than understory composition (Hanula et al. 2000a, b, Hanula and Horn 2004) and prey selection by RCWs does not appear to be contingent on understory characteristics (Hanula and Engstrom 2000, Hanula et al. 2000b). Additional research is needed to understand the relationship between groundcover, RCW foraging habitat quality, and group reproductive success.

Midstory encroachment

The negative relationships between midstory encroachment and RCW reproductive success could be explained by dense midstory impeding RCW movement among forage trees, increased resource competition associated with reduced resource partitioning, or shading of herbaceous groundcover (Convery 2002, Walters et al. 2002). Hardwood midstory encroachment may lead to less vertical separation among foraging individuals (Rudolph et al. 2007), suggesting midstory encroachment in RCW foraging habitat directly influences foraging behavior. Impeded movement among forage trees due to midstory encroachment may be particularly important for breeding females due to their tendency to forage lower on pine boles (Hooper and Lennartz 1981, Rudolph et al. 2002, Walters et al. 2002). Female RCWs appear to be more susceptible to food limitation than males, which may be an important determinant of reproductive success during the breeding season when female metabolic demands are greatest (Blancher and Robertson 1987, Daan et al. 1989, Jackson and Parris 1995).

Although midstory encroachment may influence arthropod communities, the nature of the relationship has yet to be established (Conner et al. 2004, Rudolph et al. 2007). Studies in Texas, North Carolina and South Carolina reported no difference in arthropod density or biomass related to hardwood midstory (Taylor 2003, Conner et al. 2004), whereas one study in Texas documented greater arthropod density on loblolly pine boles in stands without a hardwood midstory compared to stands with a hardwood midstory (Collins et al. 2002). Research to date suggests midstory encroachment has negative effects on RCW reproductive success, but future research is needed to explain the mechanisms involved.

Hardwood overstory

The wide range of multiple and simple linear regression coefficients and inconsistent documentation of precision estimates reported leave the magnitude of the effect of large hardwoods on RCW reproductive success uncertain. The three studies that directly examined the relationship between RCW reproductive success and the prevalence of large hardwood vegetation reported negative relationships, but did not explore the mechanisms involved (Hardesty et al. 1997, Convery 2002, Butler and Tappe 2008). Large hardwoods may indirectly reduce RCW reproductive success by limiting natural pine regeneration and herbaceous groundcover in foraging habitat, but the reported effects of these features on RCW reproductive success are themselves minimal. Furthermore, it is not clear if the negative effects of average hardwood vegetation metrics reported by Hardesty et al. (1997) and Butler and Tappe (2008) were the result of canopy or midstory hardwood vegetation in RCW foraging habitat.

Future research could assess the hypothesis that foraging RCWs expend more energy seeking suitable foraging substrate (i.e. live pines) in stands with a significant hardwood component (Repasky 1984, Hooper and Harlow 1986). Similarly, researchers could determine whether canopy closure associated with large hardwoods (i.e. ≥ 25.4 cm dbh) in RCW foraging habitat may reduce foraging habitat quality over the long term by limiting natural pine regeneration (James et al. 1997). Natural longleaf pine regeneration may be an indirect indicator of RCW foraging habitat quality due to the species' intolerance of competition from any source, especially hardwood vegetation (Wahlenberg 1946, Bruce and Bickford 1950, Smith 1955).

Pine age and size

Research on the relationship between pine size class distributions in RCW foraging habitat and reproductive success had conflicting results. Several studies showed no discernible effect on reproductive success metrics (Hooper and Lennartz 1995, Beyer et al. 1996, Wigley et al. 1999). In contrast, evidence from four studies indicated pine size class distributions in RCW foraging habitat have small, but generally consistent effects on reproductive success (Hardesty et al. 1997, James et al. 2001, Convery 2002, Walters et al. 2002). The response of RCW reproductive success to pine size class densities in foraging habitat may be contingent on additional habitat features, such as the density of old-growth pines and herbaceous groundcover (James et al. 2001). To our knowledge, the relationship between RCW reproductive success and age class densities in foraging habitat has not been examined.

Determining the respective effects of pine age and size on RCW foraging habitat quality has not been possible as these variables are highly correlated (Zwicker and Walters 1999). Larger (and presumably older) pines undoubtedly provide more foraging substrate compared to their smaller counterparts, but evidence suggests several ancillary characters of large and old pines contribute to RCW foraging habitat quality as well. The thick bark of larger and older pines may provide better arthropod microhabitat and retain large arthropods for longer periods during the day when RCWs are foraging (Hooper and Lennartz 1981, Jones and Hunt 1996, Hanula et al. 2000a). For example, wood roaches *Parcoblatta* spp. are important prey items for RCWs and often seek refuge in loose bark during the day (Hanula et al. 2000a, Horn and Hanula 2002a). Horn and Hanula (2002b) reported *Parcoblatta* spp. also are closely associated with coarse woody debris and snags, suggesting these features indirectly contribute to RCW foraging habitat quality by increasing arthropod prey availability. Large and old pines also support larger dead branches that provide additional foraging substrate and a substantial source of arthropods (Hooper 1996, Hanula and Franzreb 1998, Conner et al. 2004).

Some evidence suggests RCW reproductive success is influenced by pine size class densities but the nature of the relationship is unclear and may be contingent on additional foraging habitat features including pine density. Natural pruning occurs more rapidly in dense stands, often resulting in smaller dead branches that may support less arthropod biomass than larger dead branches (Smith 1962, Hooper 1996). Dead branch diameter is positively correlated with tree age and larger dead branches support substantial arthropod biomass, particularly wood roaches *Parcoblatta* spp., relative to other locations on longleaf pines (Hooper 1996, Hanula and Franzreb 1998). Further, high pine densities in RCW foraging habitat can decrease levels of calcium and nitrogen in the soil, which in turn may limit both nutritive value of arthropod prey and RCW reproductive success (Taylor 1986, Graveland and Van Gijzen 1994, James et al. 1997, Palik et al. 1997, Simberloff 2004). Collectively, these data suggest several features of large and old pines provide high quality foraging substrate and contribute to RCW foraging habitat quality and reproductive success.

Conclusion

The extent to which a specific habitat feature contributes to species' reproductive success is an important consideration in developing standards of habitat quality, particularly for priority species and where habitat management has broad ecological, economic, and regulatory implications. It is feasible to directly quantify many habitat features that correlate with species' reproductive success, but it is not always feasible for land managers to promote multidimensional desired habitat conditions in their entirety with limited fiscal and logistic resources. Critically evaluating the contributions of individual habitat features provides guidance for refining standards of habitat quality, future research, and development of conservation and management priorities based on features that contribute most to habitat quality.

The current definitions of good quality RCW foraging habitat include components valuable to pine ecosystems of the southern US, particularly substantial herbaceous groundcover, but inclusion of those components was not based on strong empirical evidence of relationships with RCW reproductive success. Further research is needed to demonstrate the contribution of each key foraging habitat feature to RCW foraging habitat quality and reproductive success. Of primary interest is further validation of the key foraging habitat features, associated thresholds, and recommended amount of habitat within standard foraging partitions that satisfies the requirements of the revised guidelines. We also recommend researchers focus on examining: 1) relationships between herbaceous groundcover and RCW reproductive success, 2) influence of arthropod prey availability on RCW reproductive success and how prey availability is influenced by foraging habitat features (e.g. herbaceous groundcover, snags, down coarse woody debris, midstory vegetation, and forest stand, patch and tree characteristics), 3) how interactions between structural characteristics of foraging habitat influence RCW reproductive success and foraging habitat quality (e.g. large trees ha^{-1} – small trees ha^{-1}; James et al. 2001), 4) population density dependent relationships between reproductive success and key foraging habitat features (e.g. how relationships vary along the continuum of population densities across the species' range), and 5) relationships between key foraging habitat features and other measures of productivity (e.g. survivorship or nestling weight).

A balance between exploratory and confirmatory research will help validate relationships between RCW reproductive success and components of good quality foraging habitat. Considering results of exploratory or observational studies provides guidance for the design and replication of future confirmatory studies (Johnson 2002). For example, replication of studies investigating effects of herbaceous groundcover on RCW reproductive success will help substantiate these relationships across the species' range where disparity exists between results of exploratory (Hardesty et al. 1997, James et al. 1997, 2001) and confirmatory (Spadgenske et al. 2004) studies. Ideally, these studies would be replicated over sufficient temporal (e.g. > one breeding season) and spatial (e.g. > one distinct population across the species' range) scales to minimize potential spurious results that may arise from artifacts associated with a particular site or time. If sufficient spatial or temporal replication is not possible due to fiscal or logistic constraints, we recommend studies consider unique circumstances of the study (e.g. sampling methodology, analytical approach, prevailing environmental conditions and management strategies during the study) and explicitly restrict the scope of inference when interpreting results. Inherent in our recommendations are several legal and logistical challenges for researchers. Experimental manipulation of RCW foraging habitat could have adverse effects on a population's recovery and require an incidental 'take' permit. Assuming such permitting is feasible, implementing a controlled experiment with sufficient replication of clusters including access to foraging habitat with all desired conditions likely would be difficult. Effects of individual foraging habitat features may be confounded by management practices and regional variation in habitat conditions and population density such that the contribution of key foraging habitat features to foraging habitat quality and reproductive success are not universal, but specific to regions or individual RCW populations. Further complicating foraging habitat research is the need to parse variation in reproduction from stochastic environmental events, efforts to maintain demographic stability within populations (e.g. provision of cavities and translocations), the presence/absence of helpers, and breeder experience.

We recommend future studies of RCW reproductive success and foraging habitat quality incorporate the response of reproductive success to the 2003 foraging habitat guidelines with an emphasis on identifying underlying mechanisms. If ancillary foraging habitat measurements are taken, explicit descriptions, extent and grain at which variables were summarized, and ecological reasoning regarding why the measurements were taken will facilitate: 1) replication of research, 2) understanding of underlying mechanisms, and 3) broader generalizations about relationships between foraging habitat features and RCW reproductive success (Clark and Shutler 1999, Johnson 2002). Given the complexity of the revised foraging habitat guidelines, we recommend authors critically evaluate and report effect size statistics and their precision estimates for all variables regardless of statistical significance to facilitate future quantitative reviews and meta-analyses.

Acknowledgements – We thank R. Costa, T. B. Wigley and J. I. Blake for commenting on previous versions of this manuscript. Funding was provided by the US Dept of Energy, Savannah River Operations Office through the USDA Forest Service Savannah River (Interagency Agreement DE-AI09-00SR22188) under Cooperative Agreement no. SRS 10-CS-11083601-003.

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