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Quantifying Purported Competition with Individual- and Population-Level Metrics

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Abstract: *Competitive species interactions may contribute to population declines. Purportedly, Red-bellied Woodpeckers (*Melanerpes carolinus*), a common species, and Red-cockaded Woodpeckers (*Picoides borealis*), an endangered species, compete for roosting and nesting cavities in living pine trees. To determine whether behavioral interactions measured at the individual level manifest themselves at the population level, we conducted field experiments designed to test whether the presence of Red-bellied Woodpeckers resulted in a decrease in fitness to Red-cockaded Woodpeckers. As part of a 4-year study examining the nature of interspecific interactions in two populations of Red-cockaded Woodpeckers (one stable, the Apalachicola Ranger District; one declining, the Wakulla Ranger District) in the Apalachicola National Forest, Florida, we conducted a set of Red-bellied Woodpecker removal experiments. Paradoxically, following the removal of Red-bellied Woodpeckers, we observed decreases in Red-cockaded Woodpecker group size, proportion of nests that were successful, and proportion of individuals remaining on territories. Removal of Red-bellied Woodpeckers may have exaggerated the immigration rate of Red-bellied Woodpeckers to Red-cockaded Woodpecker territories. The Red-cockaded Woodpeckers in the Apalachicola Ranger District likely can withstand pressure from immigrating Red-bellied Woodpeckers given that their population has remained relatively stable despite the presence of Red-bellied Woodpeckers. A major factor of population persistence in the Wakulla Ranger District was the high turnover rate of adult female Red-cockaded Woodpeckers, a phenomenon that was exacerbated by removal of Red-bellied Woodpeckers. Relying solely on observations of apparently competitive interactions between individuals may not necessarily provide information about population-level outcomes. Paradoxically, removing species that appear to be competitors may harm species of concern.*

Keywords: competition, *Melanerpes carolinus*, *Picoides borealis*, population, Red-bellied Woodpecker, Red-cockaded Woodpecker, removal experiment

Cuantificación de la Competencia Aparente con Medidas a Nivel Individual y Poblacional

Resumen: *Las interacciones de competencia entre especies puede contribuir a declinaciones poblacionales. Aparentemente,* Melanerpes carolinus*, una especie común y* Picoides borealis*, una especie en peligro, compiten por cavidades para descanso y anidación en árboles de pino vivos. Para determinar sí las interacciones conductuales medidas a nivel de individuo se manifiestan a nivel de la población, realizamos experimentos de campo diseñados para probar sí la presencia de* M. carolinus *resultaba en una disminución en la adaptabilidad de* P. borealis*. Como parte de un estudio de 4 años para examinar la naturaleza de interacciones interespecíficas en dos poblaciones de* P. borealis *(una estable, Distrito Apalachicola; una en declinación, el Distrito Wakulla) en el Parque Nacional Apalachicola, Florida, realizamos una serie de experimentos de remoción de* P. borealis*. Paradójicamente, después de la remoción de* P. borealis*, observamos disminuciones en el tamaño del grupo, en la proporción de nidos exitosos y en la proporción de individuos permanecientes en los territorios de* M. carolinus*. La remoción de* P. borealis *pudo haber exagerado la tasa de inmigración de* M. carolinus *a territorios de* P. borealis*. Los individuos de* P. borealis *en el Distrito Apalachicola probablemente pueden soportar la presión de los individuos de* M. carolinus *inmigrantes debido a que su población ha permanecido relativamente estable no obstante la presencia de* M. carolinus*. Un factor importante para la*

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persistencia de la población en el Distrito Wakulla fue la alta tasa de productividad de hembras adultas de P. borealis*, fenómeno que se exacerbó por la remoción de* M. carolinus*. Basarse únicamente en observaciones de interacciones aparentemente competitivas entre individuos no necesariamente proporciona información sobre resultados a nivel poblacional. Paradójicamente, la remoción de especies que aparentan ser competidoras puede dañar a especies en riesgo.*

Palabras Clave: competencia, experimento de remoción, *Melanerpes carolinus*, *Picoides borealis*, población

Introduction

There are many cases in the literature in which competitive interactions between rare species and other members of their assemblage purportedly affected the population dynamics of the rare species. For example, the distribution of the endangered Shenandoah salamander (*Plethodon shenandoah*) is limited by competitive interactions with the more common red-backed salamander (*Plethodon cinereus*) (Griffis & Jaeger 1998). Similarly, the endangered spotted-tailed quoll (*Dasyurus maculatus*) is threatened by competition with red foxes (*Vulpes vulpes*), feral cats (*Felis catus*), and wild dogs (*Canis lupus*) (Glen & Dickman 2008).

To manage rare species effectively, a framework is needed from which to understand and quantify competitive interactions. One approach used in recent investigations is to link individual behavior with population-level outcomes (e.g., Werner 1992; Beckerman et al. 1997; Relyea & Yurewicz 2002). Individual-based models of population dynamics are based on this premise (e.g., Judson 1994; Grimm 1999; DeAngelis & Mooij 2005).

To determine whether behavioral interactions measured at the individual level manifest themselves at the population level, we conducted field experiments with two species of woodpeckers, the endangered Red-cockaded Woodpecker (*Picoides borealis*) and the more common Red-bellied Woodpecker (*Melanerpes carolinus*). The experiments were designed to test whether the presence of Red-bellied Woodpeckers, a potential competitor, resulted in a decrease in fitness to Red-cockaded Woodpeckers. If the species are competing, Red-cockaded Woodpeckers should be negatively affected by the presence of Red-bellied Woodpeckers. We compared results of a sustained removal experiment with results of a short-term experimental study of individual behavior (Walters 2004).

We based our model on purported competition between Red-cockaded and Red-bellied woodpeckers for a limiting discrete resource, cavities for nesting and roosting in living longleaf pine (*Pinus palustris*) trees. The cavities were created by Red-cockaded Woodpeckers, a keystone species in pine forests of the southeastern United States (USFWS 2003). Typically, each member of a family of Red-cockaded Woodpeckers (1–5 birds) roosts individually in cavities that have been excavated by their predecessors (Conner & Rudolph 1995; Harding 1997). Over time, cavities accumulate in the cluster of cavity trees within the defended territory (Walters et al. 1988). Additional species are attracted to these cavities for roosting and nesting (Conner et al. 1997; Walters & Kneitel 2004; Blanc & Walters 2008). Virtually every cluster of cavity trees in our study area contained at least one roosting Red-bellied Woodpecker. Other birds and mammals use the cavities for reproduction. These taxa include, Eastern Bluebirds (*Sialia sialis*), Great Crested Flycatchers (*Myiarchus crinitus*), Eastern Screech-Owls (*Megascops asio*), and southern flying squirrels (*Glaucomys volans*). Still other species use the cavities for roosting, but not reproduction, including tree frogs (*Hyla* spp.), skinks (*Eumeces* spp.), and snakes (*Elaphe* spp.) (Rudolph et al. 1990; Conner et al. 1997). In many cases, these species occupy abandoned cavities, but the level of competition between flying squirrels and Red-cockaded Woodpeckers for cavities can be high (Laves & Loeb 1999). The limited number of cavities in an area is a major influence on the population dynamics of Red-cockaded Woodpeckers (Copeyon et al. 1991; Carrie et al. 1998), and the provision of artificial cavities is an important component of recovery efforts for Red-cockaded Woodpeckers (USFWS 2003).

The Red-cockaded Woodpecker typically occurs in stands of naturally regenerated, open, pine woods managed with frequent prescribed burning and thinning (James et al. 1997; Conner et al. 2001; James et al. 2004). The species has declined over most of its geographic range primarily because of habitat loss, fire exclusion, and fragmentation (Conner et al. 2001; USFWS 2003). Other factors associated with small population sizes may be accelerating population declines. We examined the influence Red-bellied Woodpeckers may have on the decline of Red-cockaded Woodpeckers. In our study area in northern Florida, Red-bellied Woodpeckers are the most abundant potential competitor (Walters 2004).

In many habitats in eastern North America, Red-bellied Woodpeckers, like Red-cockaded Woodpeckers, excavate their own cavities (Shackelford et al. 2000). In some areas of the southeastern United States where Red-bellied and Red-cockaded Woodpeckers co-occur, however, Red-bellied Woodpeckers often use Red-cockaded Woodpecker cavities. Past observations in the Apalachicola National Forest in northwestern Florida of the behavior of individual Red-bellied Woodpeckers indicate there is a high level of competition between them and Red-cockaded

Woodpeckers for cavities (Ligon 1971; Kappes & Harris 1995; Kappes 1997). Previous experimental work in the same forest, however, that examined short-term behavioral interactions between the two species indicates that when individuals of either species are removed from cavities, many cavities remain unoccupied for several days. This finding is contrary to the expectation that cavities should be reoccupied relatively quickly after a purported competitor is removed. Moreover, either species was equally likely to reoccupy a cavity (Walters 2004). Overall, the short-term experiments in the Apalachicola National Forest demonstrated that species identity of subsequent cavity occupants was surprisingly ambiguous following short-term removals and, thus, brought into question whether the species are competitors (Walters 2004).

On the basis of previous experimental observations of interactions between individuals (Walters 2004), we assessed whether behaviors of individuals have fitness consequences at the population level. To test experimentally the effect of one species on the other, we removed Red-bellied Woodpeckers from Red-cockaded Woodpecker territories. Ideally, one would perform the reciprocal removal experiment to test the effect of Red-cockaded Woodpeckers on Red-bellied Woodpeckers but this option was not feasible given the endangered status of Red-cockaded Woodpeckers.

We based our study on the following hypotheses under the premise that Red-cockaded and Red-bellied woodpeckers are competing for nest cavities. Red-cockaded Woodpecker group size (number of adult Woodpeckers; roosting or nesting Red-bellied Woodpeckers are expected to displace Red-cockaded Woodpeckers within a cluster of cavity trees); clutch size (based on the prediction that clutch size decreases when the probability of future competitive encounters is high) (Goubault et al. 2007), number of fledglings produced per year (Högstedt 1980); proportion of nests that fledge young (Högstedt 1980); proportion of nest holes reused (Loeb & Stevens 1995); and proportion of adults that remain on their breeding territory in a subsequent year (Gustafsson 1987; Merilä & Wiggins 1995) increase following removal of Red-bellied Woodpeckers.

Methods

Study Area

The Apalachicola National Forest in northern Florida (U.S.A.) is 228,865 ha and is divided into two management units, western (Apalachicola Ranger District [ARD], 116,999 ha) and eastern (Wakulla Ranger District [WRD], 111,866 ha). The forest supports 17% of all remaining Red-cockaded Woodpeckers (USFWS 2003). The western district supports an apparently stable population of 486 family groups (sensu Walters 1990) and the eastern district supports an estimated 138 family groups (USFWS 2003). The population in the eastern district is estimated to have declined by 23% from 1993 to 2003 (Walters & Kneitel 2004), which is consistent with the 26% decline from 1981 to 1990 (James 1991).

Experimental Design

The experiment was of a split-plot design. Of the 57 management compartments (i.e., areas of land within the forest managed as a unit) in the ARD that contained at least three Red-cockaded Woodpecker family groups, we randomly selected 14 (mean size = 1292 ha) for study. Within each compartment, we randomly assigned one of the clusters as a control, one to a bimonthly removal treatment (defined later) and one to a weekly removal treatment. The woodpecker groups were monitored for 2 years (June 1999–April 2001).

From among 28 management compartments in the WRD that contained at least two Red-cockaded Woodpecker family groups, we randomly selected 11 (mean = 1099 ha) for study. Within each of the 11 compartments, we randomly assigned one of the clusters as a control and one to a bimonthly removal treatment. We monitored these groups for 4 years (March 1997–March 2001).

We visited all clusters of cavity trees bimonthly at night and removed all Red-bellied Woodpeckers from cavities in which they were roosting (bimonthly and weekly treatments) by climbing to the cavity and either placing a cloth bag over the entrance so the occupant would fly into it or inserting a piece of plastic tubing with a loop on the end to move the occupant up to the entrance so it could be captured. We immediately euthanized the birds we removed with carbon monoxide. In addition, we visited weekly removal sites once per week during the day and all Red-bellied Woodpeckers observed were shot with a 20-gauge shotgun. All specimens removed were used in other studies (Foster et al. 2002; Schrader et al. 2003; Koenig et al. 2005) and then deposited in the Florida Museum of Natural History (Gainesville).

All trees containing cavities within each Red-cockaded Woodpecker territory had been inventoried and monitored since 1992. Prior to commencement of our study, we confirmed the number and location of all cavities within each experimental and control site (ARD: mean = 6.55 cavities/cluster, range = 3–10, n = 42 sites; WRD: mean = 9.95 cavities/cluster, range = 6–17, n = 22; Table 1) and that all clusters contained roosting or breeding Red-cockaded and Red-bellied woodpeckers. We surveyed cavity occupants in all sites at night by briefly shining a flashlight toward the cavity entrance while observing the cavity with binoculars. If no occupant was seen, we inserted an infrared camera mounted on the end of a 15-m telescoping fiberglass pole (Furhman Diversified, Seabrook, Texas) into the cavity to determine

Table 1. Red-cockaded Woodpecker mean (SE) productivity and number of cavities per cluster in the Apalachicola (ARD) and Wakulla (WRD) Ranger Districts (1999–2000) of the Apalachicola National Forest.

Productivity measure	District[a]	Treatment[b] weekly 1999	weekly 2000	bimonthly 1999	bimonthly 2000	control 1999	control 2000
Group size	ARD	2.3 (0.1)*	2.1 (0.1)	2.4 (0.1)*	2.4 (0.1)	2.8 (0.3)*	2.4 (0.2)
	n	14	14	14	14	14	14
	WRD	–	–	1.8 (0.3)	2.3 (0.1)	2.4 (0.2)	2.3 (0.2)
	n			11	11	11	11
Clutch size	ARD	3.3 (0.2)	3.6 (0.3)	3.3 (0.1)	3.4 (0.2)	3.4 (0.2)	3.4 (0.2)
	n	13	10	13	13	14	14
	WRD	–	–	3.3 (0.5)	3.5 (0.2)	3.4 (0.4)	3.1 (0.3)
	n			10	11	11	11
No. of fledglings	ARD	1.7 (0.3)	1.9 (0.2)	2.2 (0.2)	2.0 (0.3)	2.1 (0.2)	2.0 (0.2)
	n	14	12	13	14	14	14
	WRD	–	–	1.5 (0.3)	1.7 (0.2)	1.7 (0.2)	1.6 (0.2)
	n			10	11	11	11
No. of cavities	ARD	6.29 (0.41)		6.43 (0.39)		6.93 (0.46)	
	WRD			10.45 (1.11)		9.45 (0.53)	

[a]*Abbreviations: ARD, Apalachicola Ranger District; WRD, Wakulla Ranger District.*
[b]*Treatments: bimonthly, bimonthly removal of Red-bellied Woodpeckers; weekly, weekly removal of Red-bellied Woodpeckers; control, no removal of Red-bellied Woodpeckers (*p = 0.014, Wilcoxon signed ranks test Z = −2.449; no other tests were significant).*

whether the cavity was occupied. This method has no effect on species using cavities (Walters 2004).

In addition to nocturnal bimonthly monitoring of cavities, we visited all Red-cockaded Woodpecker groups during the nesting period (April–July) to identify the nest tree, to uniquely mark the young with color bands, and to determine group size, clutch size, and number of fledglings produced each year. We captured opportunistically any unmarked adult Red-cockaded Woodpeckers throughout the year and uniquely marked them with color bands.

Analyses

We used nonparametric tests (Wilcoxon signed rank) to compare mean adult group size, mean clutch size, and mean number of fledgling Red-cockaded Woodpeckers among control sites and bimonthly removal sites within each management compartment. We used contingency table analysis to compare the proportions of successful nests by district, treatment, and year among Red-cockaded Woodpeckers, and we used nonparametric Kruskal–Wallis tests to compare the numbers of roosting Red-bellied Woodpeckers among treatments. We compared (repeated measures analysis of variance [ANOVA]) the number of Red-bellied Woodpeckers roosting at bimonthly intervals among treatments and districts and tested for post hoc differences among treatments (Tukey's honestly significant difference [HSD]). We compared the proportion of nest holes reused in successive years among treatments and districts (χ^2 tests). In the WRD, we tested for differences (Wilcoxon signed rank tests) in the number of years a nest tree was used for nesting by treatment and tested for differences (logit loglinear model) in the proportion of banded Red-cockaded Woodpeckers that remained on their breeding sites by district from 1999 to 2000. All statistical tests were conducted in SPSS (SPSS 2000).

Results

Before initiating the Red-bellied Woodpecker removal experiment in the ARD, we determined that the numbers of Red-bellied Woodpeckers in each treatment (control, bimonthly, weekly) were not statistically different (Kruskal–Wallis, $p = 0.193$). In the WRD, we removed Red-bellied Woodpeckers bimonthly at the rate of 0.71 birds·site^{-1} ·month^{-1} from May 1999 through March 2001 (Fig. 1). In the ARD, we removed 0.35 birds·site^{-1}·month^{-1} (49% less than the WRD) in biomonthly removals from June 1999 to April 2001. Also in the ARD, we removed 0.48 birds·site^{-1}·month^{-1} (37% more than in the bimonthly removal treatment) in weekly removals over the same period. The number of Red-bellied Woodpeckers removed per site increased over time (Fig. 1). Our removal of birds significantly reduced the number of Red-bellied Woodpeckers in each of our bimonthly treatments (repeated measures ANOVA; ARD: $p = 0.003$; WRD: $p = 0.021$; Fig. 2), but did not eliminate them. In the ARD, the number of Red-bellied Woodpeckers present in bimonthly and weekly removal treatments differed from the control (bimonthly: $p = 0.037$; weekly: $p = 0.003$, post hoc Tukey's HSD) but not from each other ($p = 0.578$). The two districts differed in the number of Red-bellied Woodpeckers present in control and removal plots ($p < 0.001$), but there was no treatment by district effect ($p = 0.295$).

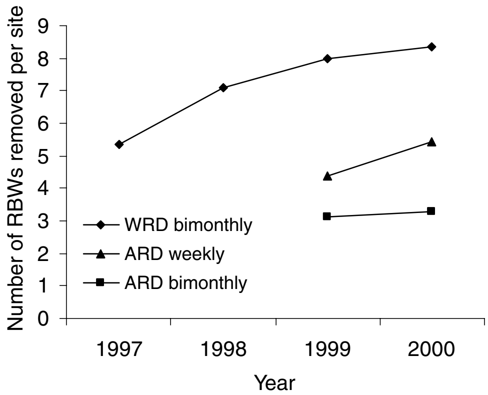

Figure 1. Mean number of Red-bellied Woodpeckers (RBWs) removed per site by treatment and district (ARD, Apalachicola Ranger District; WRD, Wakulla Ranger District). The values for ARD 1999 are adjusted because removal did not begin until June. Error bars are excluded for clarity of presentation.

The experimental removal of Red-bellied Woodpeckers had a significant negative effect on Red-cockaded Woodpecker group size in the ARD in 1999 (Wilcoxon signed ranks test $Z = -2.449$, $p = 0.014$; Table 1) and a nonsignificant negative effect in the ARD in 2000 ($Z = -1.941, p = 0.052$). There was no other statistically significant effect of the removal of Red-bellied Woodpeckers on group size of Red-cockaded Woodpeckers in the WRD or on clutch size or number of young fledged in either district (Table 1). There was, however, a negative effect of removal of Red-bellied Woodpeckers in 1999 on the proportion of nests of Red-cockaded Woodpecker that successfully fledged young in both districts (ARD: $\chi^2 = 6.239$, $p = 0.044$; WRD: $\chi^2 = 4.701$; $p = 0.030$; Table 2).

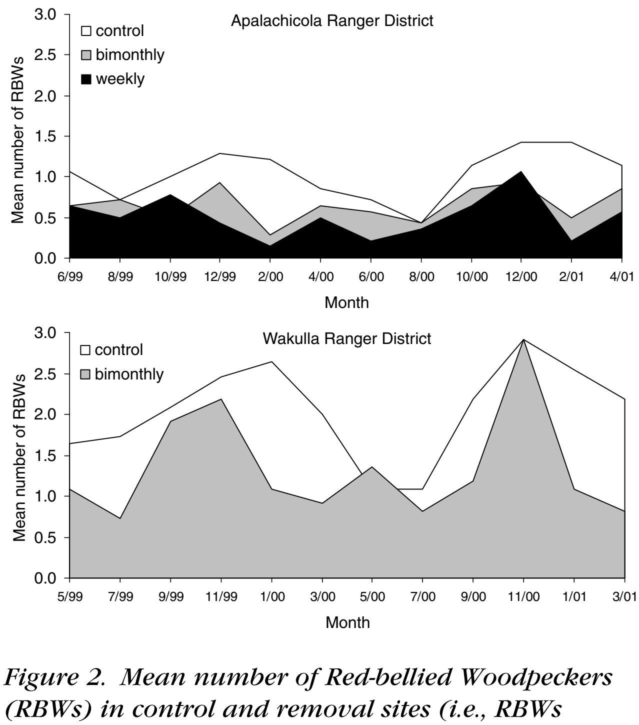

Figure 2. Mean number of Red-bellied Woodpeckers (RBWs) in control and removal sites (i.e., RBWs removed from the site) for the Apalachicola and Wakulla ranger districts. Error bars are excluded for clarity of presentation.

There was no difference in the proportion of nest trees that were reused in 2 successive years (1999–2000) among treatments or districts (ARD: $\chi^2 = 0.329$, $p = 0.848$; WRD: $\chi^2 = 0.114$, $p = 0.735$; Table 2). Likewise, the number of years a given nest tree was used did not differ between the treatments in the WRD when we compared 1998–2000 with 2001–2003 ($Z = -0.141$, $p = 0.888$).

The proportion of adult breeding Red-cockaded Woodpeckers remaining in consecutive years was higher in the ARD (logit likelihood ratio $\chi^2 = 12.086$, df $= 5$, $p = 0.034$; Table 2). In our removal treatments in the WRD, both the proportion of males and females remaining from 1 year to the next decreased compared with controls, the latter by almost 50%. The proportion of males in the ARD remaining from year to year did not differ among treatments. Nevertheless, in weekly and bimonthly removal treatments in the ARD, females were less likely to remain from 1 year to the next in sites where Red-bellied Woodpeckers had been removed.

Removal effort in year 1 in the WRD was not as intensive as in later years. Over the 4 years, the number of Red-cockaded Woodpeckers in removal clusters was lower than the number in control clusters. Intermonthly variation in number of Red-cockaded Woodpeckers was larger in control groups (Fig. 3a). Nevertheless, the number of Red-bellied Woodpeckers was similar in removal and control plots (Fig. 3b). The pattern of seasonal peaks in abundance of Red-bellied Woodpeckers in spring and autumn observed for 1999–2001 was also evident in 1997–2001. The birds we removed in winter were quickly replaced, but those removed in late spring were not. In control clusters, the abundance of Red-cockaded Woodpeckers rose following a drop in abundance of Red-bellied Woodpeckers from mid-1998 onward (Fig. 3c).

Discussion

Despite the intensity and length of our removal experiment, we were unable to remove Red-bellied Woodpeckers completely. Paradoxically, group size, proportion of nests that fledged young, and proportion of individuals remaining on the breeding territory decreased after removal of Red-bellied Woodpeckers, contrary to expectation. Removal of Red-bellied Woodpeckers, thus, had a strong negative effect on Red-cockaded Woodpeckers. We do not think it is accurate to conclude that our results

Table 2. Proportions of successful nests, nest trees reused, and breeders remaining at breeding sites for Red-cockaded Woodpeckers by district, year, and sex in sites where Red-bellied Woodpeckers were removed bimonthly or weekly compared with control sites.

			Treatment[b]				
Metric	*District*[a]	*Year*	*weekly*	*bimonthly*	*control*	χ^2	p
Proportion of successful nests	ARD ($n = 14$)	1999	0.50	0.64	0.93	6.239	0.044
		2000	0.64	0.79	0.79	0.985	0.611
	WRD ($n = 11$)	1998	–	0.45	0.64	0.733	0.392
		1999	–	0.36	0.82	4.701	0.030
		2000	–	0.82	0.73	0.259	0.611
		2001	–	0.73	0.64	0.210	0.647
Proportion of nest trees reused	ARD	1999–2000	0.73 ($n = 11$)	0.67 ($n = 12$)	0.77 ($n = 13$)	0.329	0.848
	WRD	1999–2000	–	0.80 ($n = 5$)	0.71 ($n = 7$)	0.114	0.735
Proportion remaining at breeding site[c] (male [n], female [n])	ARD	1999–2000	0.82 (11), 0.60 (5)	0.91 (11), 0.57 (7)	0.85 (13), 1.00 (5)		
	WRD	1999–2000	–, –	0.60 (10), 0.20 (10)	0.78 (9), 0.44 (9)		

[a] *Abbreviations: ARD, Apalachicola Ranger District; WRD, Wakulla Ranger District.*
[b] *Treatments: bimonthly, bimonthly removal of Red-bellied Woodpeckers; weekly, weekly removal of Red-bellied Woodpeckers; control, no removal of Red-bellied Woodpeckers.*
[c] *Logit loglinear analysis: variable district (likelihood ratio $\chi^2 = 12.086$, p $= 0.034$), variable sex (likelihood ratio $\chi^2 = 9.812$, p $= 0.081$), variable treatment (likelihood ratio $\chi^2 = 6.558$, p $= 0.256$); all interaction effects p > 0.100.*

demonstrate that Red-bellied Woodpeckers have a positive effect on Red-cockaded Woodpeckers. We believe there is an alternative explanation for our results.

Once Red-bellied Woodpeckers were removed, new conspecific individuals within the population immigrated consistently into our experimental sites. Our observations suggest that the immigrating Red-bellied Woodpeckers affected Red-cockaded Woodpeckers negatively. In the declining WRD population in control sites, 44% of female Red-cockaded Woodpeckers remained from 1 year to the next (less than half the proportion of females that remained in ARD control sites). Where Red-bellied Woodpeckers were removed in the WRD, only 20% of female Red-cockaded Woodpeckers remained from 1 year to the next. It appears that immigrating Red-bellied Woodpeckers had an additional (relative to control sites) severe effect on the persistence of female Red-cockaded Woodpeckers. Male Red-cockaded Woodpeckers (breeders and helpers) are dominant to female Red-cockaded Woodpeckers, so it follows that females should roost in cavities that are suboptimal for males (Jackson 1994). Red-bellied Woodpeckers are either more successful at competing with female Red-cockaded Woodpeckers or the types of cavities relegated to female Red-cockaded Woodpeckers are more attractive to Red-bellied Woodpeckers. In contrast, Red-bellied Woodpeckers in control sites remained relatively faithful to the cavities they occupied (Walters 2004) and thus created a relatively stable environment. Resident Red-bellied and Red-cockaded woodpeckers that are "familiar neighbors" likely have established their preferred cavities and, thus, have reduced conflict between species (sensu "dear enemies," Temeles 1994). Naive Red-bellied Woodpeckers that immigrate into a Red-cockaded Woodpecker cavity cluster are likely to increase instability among cavity occupants because they search out cavities in which to roost or nest without having knowledge of established cavity preferences.

Over twice as many Red-bellied Woodpeckers were removed from the WRD than from the ARD per unit effort and the number of trees with available cavities per cluster was 36% higher in the WRD than in the ARD (Table 1). Paradoxically, the rate at which cavities are constructed is lower in the WRD than the ARD (James et al. 1995). The discrepancy is likely due to reduced levels of prescribed fire frequency in the WRD, where dead trees with cavities remain standing longer rather than being consumed during prescribed fires. A lack of fire in pine forests also allows the proportional abundance of hardwoods to increase, a vegetation type favored by Red-bellied Woodpeckers (Shackelford et al. 2000). Given a sufficient number of cavity trees within a Red-cockaded Woodpecker cluster, more than one pair of Red-bellied Woodpeckers can be present.

By removing Red-bellied Woodpeckers on a weekly basis in the ARD, we increased the number of birds removed by 37% over the number removed during bimonthly visits. But the number of Red-bellied Woodpeckers removed was still lower than for those sites in the WRD where removals were conducted only every 2 months. Apparently, there is a remarkably high abundance of Red-bellied Woodpeckers available to immigrate to available sites in the WRD, especially from November to March, when young of the year are dispersing.

We do not think our findings are an artifact of our methods. Firearms were discharged only in weekly removal treatments and so did not affect paired comparisons between bimonthly removals and controls. Furthermore, none were fired when Red-cockaded Woodpeckers were detected within the cluster. The sound from the discharge would be heard relatively equally among the

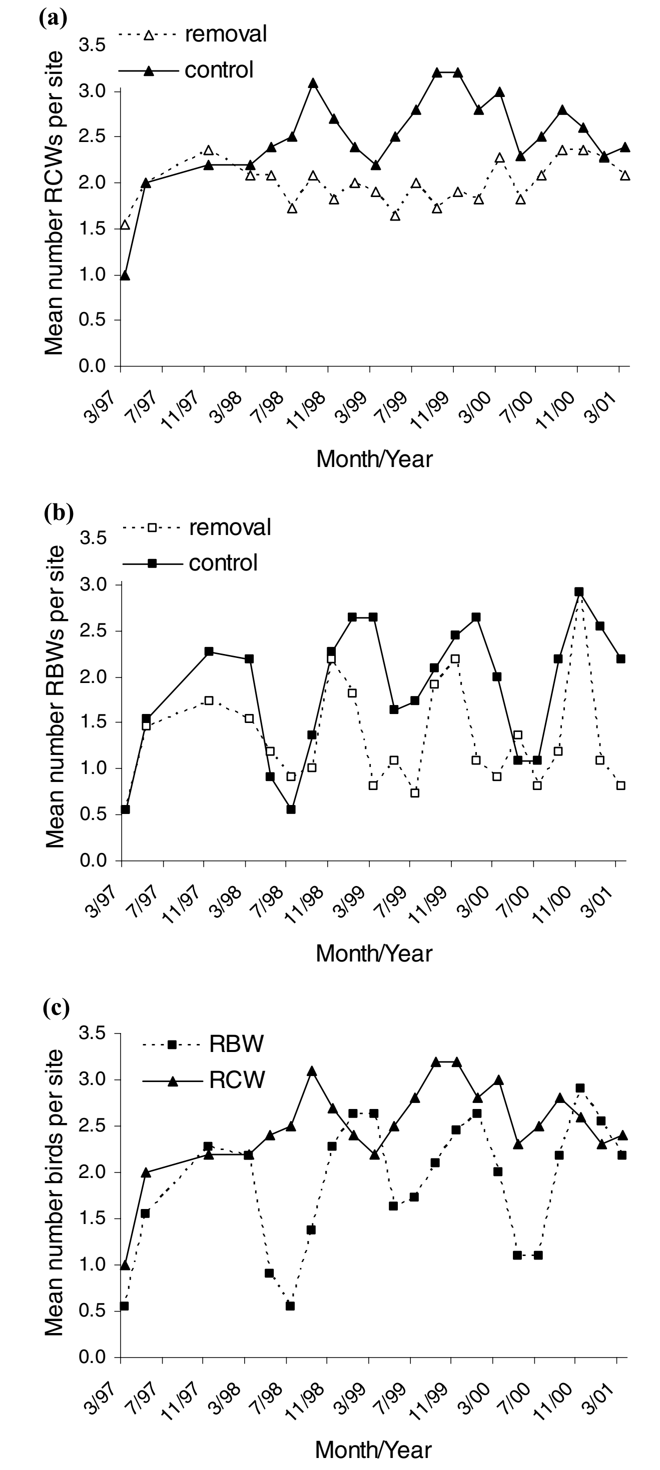

Figure 3. The mean number of (a) Red-cockaded Woodpeckers (RCW) per site by treatment in the Wakulla Ranger District, (b) Red-bellied Woodpeckers (RBW) per site by treatment in the Wakulla Ranger District, and (c) Red-cockaded Woodpeckers and Red-bellied Woodpeckers in control sites (treatments: removal, removal of RBW bimonthly from sites [$n = 11$*]; control [*$n = 10$*], no removal of RBW). Error bars are excluded for clarity of presentation.*

three treatments because all clusters were relatively close to one another. Hunting occurs in the study area; thus, the birds were accustomed to the sound of gunshots.

We spent an average of 27 min longer in bimonthly removal plots in the WRD and 10 and 11 min longer in ARD bimonthly and weekly removal plots, respectively, than in control plots. We do not believe a 10-min difference in visit duration explains the difference between treatment groups. The other difference among treatments was that we used ladders to climb trees in removal plots at night. We do not believe the act of carrying ladders would have any effect beyond that experienced by surveying the cavities with a flashlight and camera, as was done for all treatments. Ladders are used routinely throughout the Red-cockaded Woodpeckers' range during the breeding season to monitor nesting without any effect, and roosting birds are exposed to many loud sounds at night in our study area (e.g., frogs, owls, gunfire, traffic, thunder).

Moreover, if the act of removing Red-bellied Woodpeckers disturbed Red-cockaded Woodpeckers, we would have expected a decrease in Red-cockaded Woodpecker group size in removal plots in both districts, but removals only negatively affected group size in the ARD, where we spent less than half as much time per survey on average. Thus, disturbance associated with the act of removing Red-bellied Woodpeckers does not adequately account for our results.

In the WRD we tracked the relative abundances of Red-bellied Woodpeckers and Red-cockaded Woodpeckers over 4 years in control clusters. Increases in Red-bellied Woodpecker abundance were generally followed by decreases in the abundance of Red-cockaded Woodpeckers. This could mean the species are competing for cavities and that the number of cavities is limiting.

To understand the full extent of the nature of competitive interactions, it is important to consider the differences between experimental approaches that examine individuals and those that examine populations. Results of previous studies of individuals show reciprocal outcomes of competition experiments between the two species (Walters 2004). Our results show that adult female Red-cockaded Woodpeckers are strongly and negatively affected by the removal of Red-bellied Woodpeckers, likely due to the immigration of Red-bellied Woodpeckers. This population-level effect, which we exaggerated through experimental manipulation, is probably contributing to the population decline of Red-cockaded Woodpeckers in the WRD. A third approach, which is beyond the scope of this study, is to examine species interactions at the community level, thereby including indirect pathways between the two focal species that might be mediated through a third species, such as the southern flying squirrel (Walters 2004; Blanc & Walters 2008; Kappes 2008).

The results of a previous study in this forest (Kappes 1997), which was based primarily on observations, labeled Red-bellied Woodpeckers "kleptoparasites" because Red-cockaded Woodpeckers excavate the cavities that Red-bellied Woodpeckers subsequently use. Kappes viewed the interaction as asymmetrical. His argument is that Red-cockaded Woodpeckers are negatively affected by Red-bellied Woodpeckers because Red-bellied Woodpeckers usurp the cavities Red-cockaded Woodpeckers create. Red-bellied Woodpeckers, he argues, benefit because they obtain cavities without expending the energy associated with excavation. We further document the negative effect of Red-bellied Woodpeckers on Red-cockaded Woodpeckers, but we did not test whether Red-cockaded Woodpeckers have a positive effect on Red-bellied Woodpeckers.

Observations of behavioral interactions, although important, should not be generalized to the population level until experiments can be conducted to clarify the fitness consequences of purported competition at individual or population levels. An example of the disconnect between observations of individuals and population outcomes was provided by Koenig (2003). He illustrated how anecdotal observations of European Starlings (*Sturnus vulgaris*) taking over cavities of native species are common, but, when quantified at the regional scale, there was little evidence of population-level declines in areas where starlings and native species co-occur. In our study system, researchers came to different conclusions on the basis of observations of interactions between individuals. Anecdotally, Red-bellied Woodpeckers, like the starlings, appeared to have a strong negative effect on Red-cockaded Woodpeckers as illustrated by observations of cavity usurpation (Kappes 1997). But, when quantified with experiments, the probability of the two species' taking over each other's cavities was relatively equal (Walters 2004). The population-level results we report here support Kappes' anecdotal observations rather than those obtained through controlled experiments at the individual level.

The Red-bellied Woodpecker, a native species that has been expanding its geographic range for decades in all forests in the eastern United States, may be affecting numerous other species that occupy cavities of similar size. Removal of Red-bellied Woodpeckers in an attempt to reduce competitive interactions with endangered Red-cockaded Woodpeckers may cause more harm than good because of the disruptive nature of Red-bellied Woodpecker immigration. A similar removal approach is currently being considered for Barred Owls (*Strix varia*), a native species that has recently expanded its range and purportedly is competing with Spotted Owls (*S. occidentalis*), a threatened species (Gutiérrez et al. 2007). Relying solely on observations of apparently competitive interactions between individuals may not necessarily provide information on population-level fitness consequences of such interactions.

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