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Estimating Species Interactions in a Woodpecker Tree-Hole Community at the Individual, Population, and Community Levels

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THE FLORIDA STATE UNIVERSITY
COLLEGE OF ARTS AND SCIENCE

ESTIMATING SPECIES INTERACTIONS IN A WOODPECKER TREE-HOLE
COMMUNITY AT THE INDIVIDUAL, POPULATION, AND COMMUNITY LEVELS

By

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To Julie Jo

Thanks for your love, support, and patience through all of this

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ABSTRACT

The endangered red-cockaded woodpecker (*Picoides borealis*) is a keystone species in the southeastern United States where it excavates tree holes in living pines trees. An understanding of the interactions among the species using the tree holes may indicate whether they affect red-cockaded woodpeckers negatively. In the Apalachicola National Forest of northern Florida, I conducted a series of experiments at the individual, population, and community level to determine the nature of these interactions. Short-term interactions at the individual level were quantified by removing red-cockaded woodpeckers and red-bellied woodpeckers (*Melanerpes carolinus*), the two numerically dominant species in the assemblage and by temporarily occluding tree holes. Reciprocal effects of each species on the other were demonstrated over periods as short as 48 hours. Surprisingly, at the population level, red-cockaded woodpecker group size and female persistence were reduced in areas where red-bellied woodpeckers were removed. The immigration rate of floater red-bellied woodpeckers was inadvertently increased and thereby increased the disruption within red-cockaded woodpecker family groups. At the community level, Markov models were used to measure the interaction among members of the species assemblage. Time and location did not affect the matrix transition probabilities. In a district of the forest where the red-cockaded woodpecker population is declining, the removal of red-bellied woodpeckers allowed the population of flying squirrels (*Glaucomys volans*) to increase. In a district where the red-cockaded woodpecker is stable, the removal of red-bellied woodpeckers did not have any effect. When matrices were projected at equilibrium, 50% more red-cockaded woodpeckers and 50% less red-bellied woodpeckers were predicted in the stable population than in the declining population. The interaction of

both red-bellied woodpeckers and flying squirrels with red-cockaded woodpeckers is probably contributing to the decline of red-cockaded woodpeckers in parts of the Apalachicola National Forest and possibly elsewhere. This study underscores the need for a combination of empirical approaches that allow investigators to identify mechanisms of species interactions at the individual level, the fitness effects at the population level, and the overall effects on the assemblage at the community level.

INTRODUCTION

The study system that I describe is that of the endangered keystone species, the red-cockaded woodpecker (*Picoides borealis*, USFWS 2003). A species of the fire-prone pine forests of the southeastern United States, the red-cockaded woodpecker has evolved the ability to excavate tree holes in living pine trees. Presumably, by excavating a roost and nest hole in a living, as opposed to a dead tree, the propensity for the tree to be consumed during a fire is diminished (Conner et al. 2001). The excavation process can take many years. Red-cockaded woodpeckers may have evolved their habit of cooperative breeding in response to the scarcity of tree holes in which to nest (Conner and Rudolph 1995a, Harding 1997). Male offspring either disperse or remain with their parents as helpers. Helper males contribute to raising subsequent young and they can inherit their father's territory when he dies (Walters et al. 1988). In addition to the length of time that it takes to excavate a tree hole, red-cockaded woodpeckers have also evolved the behavior of creating resin wells on the surface of the tree's bark in the vicinity of the tree-hole entrance. This habit deters arboreal snakes from climbing the tree and depredating the young or the adult within the tree hole (Rudolph et al. 1990). In sum, tree holes in living pine trees are a critical resource for red-cockaded woodpeckers.

Over time, tree holes accumulate in the cluster of trees in the center of a territory (Walters et al. 1988) and a suite of additional species is attracted to them (Conner et al. 1997, Walters and Kneitel 2004). Besides red-cockaded woodpeckers, vertebrate species that use the tree holes for reproduction include other birds (red-bellied woodpeckers [*Melanerpes carolinus*], eastern bluebirds [*Sialia sialis*], great crested

flycatchers [*Myarchus crinitis*], eastern screech owls [*Otus asio*]), and mammals (southern flying squirrel [*Glaucomys volans*]). Other vertebrate species that use the tree holes for roosting, but not reproduction, include tree frogs (*Hyla* sp.), skinks (*Eumeces* sp.), and snakes (*Elaphe* sp., Rudolph et al. 1990, Conner et al. 1997).

With changing land use and timber harvest, red-cockaded woodpeckers have declined over most of their geographic range (Conner et al. 2001). Since 1973, they have been listed as a federally endangered species. As the populations have declined, other ecological factors may come into play. Competition with other tree-hole users is believed to be a contributing factor to the decline of red-cockaded woodpeckers in some areas (USFWS 2003).

This study examines the potential competitive interactions that may exist between red-cockaded woodpeckers and other members of the assemblage of birds and other animals that roost in tree holes excavated by red-cockaded woodpeckers. I am particularly interested in testing the nature of the interactions between the two most numerically dominant species, the red-cockaded woodpecker and the red-bellied woodpecker. Red-bellied woodpeckers, like red-cockaded woodpeckers, are primary tree-hole nesters. They are found in many habitats in eastern North America (Shackelford et al. 2000). In areas where red-bellied and red-cockaded woodpeckers occur together, red-bellied woodpeckers apparently prefer to roost at night or nest in red-cockaded woodpecker tree holes rather than excavating their own tree holes in dead trees. Previous observations of individual behavior had suggested that red-bellied woodpeckers are strong competitors for red-cockaded woodpecker tree holes (e.g. Ligon 1971, Kappes and Harris 1995, Kappes 1997).

The study site for my experimental work is the Apalachicola National Forest in northern Florida. This 228,865 ha forest is divided into two management units, a western one (Apalachicola Ranger District [ARD], 116,999 ha) and an eastern one (Wakulla Ranger District [WRD], 111 866 ha). As a whole, the forest supports 17% of all remaining red-cockaded woodpeckers (USFWS 2003). The ARD supports an estimated 486 family groups and that population appears to be stable. The WRD

supports an estimated 138 family groups (USFWS 2003) and its population has been estimated to have declined by 20% in the past 5 years (USFS results). By conducting my studies in both management districts, I hoped to detect differences in their population dynamics and to clarify the nature of species interactions between the red-cockaded woodpecker and its most ardent competitor.

Chapter 1 is a set of experiments that examines the nature of the interactions between individual red-cockaded woodpeckers and red-bellied woodpeckers. I conducted a series of occlusion experiments in which individual red-cockaded or red-bellied woodpeckers were prevented from entering their normal roost hole. I forced the individuals to choose among the remaining tree holes in the cluster of trees associated with that red-cockaded woodpecker family group, or to take the alternative of not using any tree hole in the cluster. After a short period, I removed the barrier and allowed the bird to return. In a second set of experiments I removed red-cockaded and red-bellied woodpeckers. The hypothesis being tested was whether red-bellied woodpeckers are competitively dominant to red-cockaded woodpeckers. By removing individuals, I created an opportunity for a subordinate species to move into the vacated tree hole. In collaboration with a United States Department of Agriculture Forest Service's translocation program, I was also able to study shifts in tree-hole occupancy after juvenile red-cockaded woodpeckers were removed from their natal sites.

Chapter 2 examines interactions between red-cockaded woodpeckers and red-bellied woodpeckers from the population-level perspective. I removed red-bellied woodpeckers from red-cockaded woodpecker clusters bimonthly and weekly. I measured the response to the removals by examining the group size, clutch size, and fledging success of red-cockaded woodpeckers and I compared my findings with control sites. I surveyed sites at night for up to 4 years and determined the occupancy of all tree holes in the experimental clusters.

Chapter 3 offers a third perspective on species interactions. In this study, I examined the effect of red-bellied woodpecker removals on the entire species assemblage associated with red-cockaded woodpecker clusters. By surveying the tree-hole

occupants bimonthly for 2 years I was able to generate transition matrices that allow me to compare the overall scope of interactions among species. I was able to compare how the species dynamics differ between management districts on the forest and among removal treatments.

1. THE ROLE OF INDIVIDUAL BEHAVIOR IN COMPETITIVE OUTCOMES IN THE SPECIES ASSEMBLAGE OF WOODPECKER TREE HOLES

Introduction

A recent body of literature has examined the role of individual behavior on population-level outcomes (e.g. Werner and Anholt 1996). In particular, trait-mediated interactions (e.g. behavior) have emerged as important determinants of population-level effects (Werner 1992, Beckerman et al. 1997, Relyea and Yurewicz 2002). Because interactions among species actually take place between individuals, it follows that studies of population interactions should be supplemented with studies of short-term behavioral interactions among individuals (Martin 1986, Tilman 1987, Łomnicki 1988).

I quantified the short-term interactions among individual organisms within an assemblage that use tree holes in longleaf pine (*Pinus palustris*) trees for roosting and nesting. Red-cockaded woodpeckers (*Picooides borealis*), an endangered non-migratory keystone species in the longleaf pine ecosystem, create holes in living pines (USFWS 2003). These holes can take from 6 to 15 years to complete (Conner and Rudolph 1995a, Harding 1997). Tree holes are typically constructed in mature trees that are greater than 100 years old (Hovis and Labisky 1985, Rudolph and Conner 1991, James et al. 1997). Once created, the tree holes can be used for up to 30 years by successive generations of red-cockaded woodpeckers (Conner and Rudolph 1995a). However, as tree holes age, red-cockaded woodpeckers are increasingly likely to abandon them and create newer holes in other trees. Over time, the tree holes accumulate in the defended area of a family group and the trees with tree holes are referred to as a "cluster"

(Walters et al. 1988). Here I consider the assemblage of species that use tree holes excavated by red-cockaded woodpeckers (the only species capable of excavating living pine trees) in the Apalachicola National Forest in northern Florida. Having a discrete resource such as tree holes makes experimental manipulation tractable and makes the system conducive to investigations of competitive interactions among members of the assemblage.

Red-cockaded woodpeckers are cooperative breeders that remain as a family group throughout the year (Ligon 1970). Cooperative breeding in this species may have evolved in response partly to a limited number of available tree holes. Because red-cockaded woodpeckers live in a fire-maintained ecosystem, building tree holes in dead trees (like most woodpeckers do) would not be a viable option because of the propensity of the dead trees to be consumed during frequent fires. Thus red-cockaded woodpeckers may have evolved the ability to create tree holes in living pines because the living trees are relatively tolerant of frequent fires and they provide safe nest and roost sites for individual woodpeckers (Conner et al. 2001). Each individual in the family group roosts in a separate tree hole each night.

Reasons for leaving a particular tree hole can include usurpation by another individual (Ligon 1970), juvenile dispersal away from the family group (Lennartz et al. 1987), damage to the hole or tree from fire or decay (Conner and Locke 1979), inundation of the hole with rainwater (Walters and Kneitel 2004), death to the tree from beetle infestation (Conner and Rudolph 1995b), breakage of the tree at the hole from wind damage (Conner et al. 1991, Conner and Rudolph 1995c), or death or deterioration of the tree from natural causes (Ligon 1970).

A variety of species other than red-cockaded woodpeckers (e.g. other birds, mammals, amphibians, reptiles, and invertebrates) use these tree holes for roosting or nesting, both in the living trees and after the trees die. No other species besides red-cockaded woodpeckers excavates tree holes in living pine trees so the red-cockaded woodpecker is integral to the assemblage and is considered a keystone species (USFWS 2003). Some of the other excavating species in the assemblage can enlarge

pre-existing tree holes to facilitate their preferred dimensions while others must wait until trees die in order to be able to excavate the softer wood. The tree hole changes over time, and its progression can be viewed as a processing chain (*sensu* Heard 1994). The changes occur because of modifications made to the hole by occupants (i.e. consumer-dependent processing) and through decay and weathering (i.e. consumer-independent processing). The entrance diameter of a tree hole appears to be one of the best predictors of the species that will use it (Conner et al. 1996, pers. obs). Thus, species that enlarge smaller tree holes are providing a new resource to those that use larger tree holes.

The species that used tree holes in the Apalachicola National Forest in order of increasing preferred hole size were: red-bellied woodpecker (*Melanerpes carolinus*), southern flying squirrel (*Glaucomys volans*), migratory eastern bluebird (*Sialia sialis*), migratory great crested flycatcher (*Myiarchus crinitus*), eastern screech owl (*Otus asio*), and pileated woodpecker (*Dryocopus pileatus*, pers. obs.). Other species found using red-cockaded woodpecker tree holes include red-headed woodpecker (*Melanerpes erythrocephalus*), northern flicker (*Colaptes auratus*), brown-headed nuthatch (*Sitta pusilla*), squirrel tree frog (*Hyla squirella*), gray rat snake (*Elaphe obsoleta spiloides*), corn snake (*Elaphe guttata*), broad-headed skink (*Eumeces laticeps*), and various Hymenoptera.

In general, tree holes are known to be limiting to bird populations that use them (Dhondt and Eyckerman 1980, Newton 1994). If tree holes are limiting to an entire assemblage of animals that use them, competition for tree holes within and among species is expected to occur. If species use holes with specific characteristics (e.g. tree-hole diameter), one would expect competition to be more intense among species using holes with similar characteristics. For example, red-bellied woodpeckers compete directly with red-cockaded woodpeckers for small diameter tree holes (Kappes and Harris 1995). A second factor that could influence the intensity of interactions among the assemblage of resident species is seasonal pulses of migratory species. During the summer months, the species richness and occupancy rate of tree holes are expected to

be high because migratory species (e.g. eastern bluebird, great crested flycatcher) join the species assemblage. Thirdly, tree-hole occupancy is expected to increase late in the breeding season because newly fledged juvenile birds are seeking tree holes for roosting at night (Conner et al. 1996). Juvenile red-cockaded woodpeckers roost in tree holes in their natal cluster several weeks after leaving their nest hole (Ligon 1970). If no tree holes are available some juveniles may roost outside of tree holes for months until one becomes available or they disperse to another cluster (Hooper and Lennartz 1983). Similarly, other resident species fledge young that seek holes. One of the hypotheses proposed to account for the decline of the red-cockaded woodpecker rangewide is competition for tree holes from other members of the assemblage (USFWS 2003). My goal was to assess whether such competition is occurring in the Apalachicola National Forest and, if so, to determine the mechanism by which competitors interact with endangered red-cockaded woodpeckers.

In the Apalachicola National Forest, the most numerous of the occupants of tree holes excavated by red-cockaded woodpeckers are red-cockaded woodpeckers (~40% of tree-hole occupants), followed by red-bellied woodpeckers (~16%), and southern flying squirrels (~9%, Walters unpub ms). Red-bellied woodpeckers are very common in this forest and are found in almost every cluster where red-cockaded woodpeckers occur. I have assumed that the numerically dominant species and those species that prefer the smallest size class of tree-hole diameters are the most likely members of the assemblage to interact. Here I test whether competition is occurring among these two most numerically dominant species, red-cockaded woodpeckers and red-bellied woodpeckers, and I examine how this interaction may affect other members of the assemblage. By conducting experimental manipulations of tree-hole occupants, I hope to discover how hole occupants interact.

I performed three experiments: (1) I reduced the number of red-cockaded woodpeckers, (2) I reduced the number of red-bellied woodpeckers, and (3) I reduced the availability of tree holes. If interspecific competition were occurring, I expected a

different species to occupy the vacant tree hole. Finally, if no competition was occurring, I expected a tree hole from which I had removed a bird to remain empty.

Materials and methods

I conducted three experiments in the Apalachicola National Forest in northern Florida (USA). This 228 865 ha forest, divided into a western (Apalachicola Ranger District [ARD], 116 999 ha) and an eastern (Wakulla Ranger District [WRD], 111 866 ha) unit. As a whole it supports 17% of all remaining red-cockaded woodpeckers (USFWS 2003). In 2000, the ARD population was estimated to support 486 family groups and was deemed "recovered" by the USFWS (USFWS 2003). The WRD is estimated to support 138 family groups and appears to be declining (USFWS 2003, pers. obs.).

Clusters used for the red-cockaded woodpecker removals (Experiment 1) were selected from among the approximately 150 clusters that were monitored each year by the United States Department of Agriculture Forest Service. For the other experiments, fourteen management compartments ($\bar{X} = 1\,292$ ha) were randomly selected from among 57 compartments that contained at least four red-cockaded family groups in the ARD. Employing a split plot design, I randomly assigned one of the clusters in each compartment to a control group, two to a red-bellied woodpecker removal group (Experiment 2), and one to an occlusion group (Experiment 3). All red-cockaded woodpecker groups used in this study had been monitored during the nesting periods of 1999—2000, before any manipulations took place. I located all tree holes ($\bar{X} = 6.9$ tree holes per cluster, range = 4–10) and monitored the number of red-cockaded woodpecker adults in the social group and the number of young to successfully fledge from the nest. For other species I recorded their presence in tree holes.

Tree-hole occupants were identified at night from the ground by shining a flashlight towards the tree-hole entrance and observing the entrance for any occupants that peered outwards. If no occupants were apparent using the first method, an infrared camera mounted on the end of a 15-m telescoping fibreglass pole (Furhman Diversified,

Inc.; Seabrook, Texas, USA) was inserted into the tree hole. Due to limitations of the inventory methods, occupants could only be identified to species. It was not possible to determine the sex or age of occupants without excessive disturbance.

Experiment 1 — Removal of juvenile red-cockaded woodpeckers

As part of the U.S. Forest Service / United States Fish & Wildlife Service red-cockaded woodpecker translocation program, juvenile red-cockaded woodpeckers are removed each autumn from candidate woodpecker groups in the ARD and transported to other smaller populations throughout the southeastern United States (Hess and Costa 1995). In my study, male and female juvenile red-cockaded woodpeckers were removed from 23 and 24 groups, respectively, in the autumn of 1999 and 2000. Juvenile males were removed only from groups that had at least one other nonbreeding male present (i.e. adult helper male or juvenile male). Clusters used for translocation had been surveyed to establish red-cockaded woodpeckers' group size and the location of tree holes used by juveniles prior to capture.

To evaluate intraspecific competitive interactions among red-cockaded woodpeckers and interspecific interactions with other members of the assemblage, I worked collaboratively with the translocation program. Individual juvenile red-cockaded woodpeckers were removed from their respective tree holes (hereafter referred to as the "focal tree hole") and I considered the cluster to be the experimental unit. I surveyed clusters on the night that juvenile woodpeckers were captured for relocation to determine all occupants of available tree holes. Clusters were revisited 2–9 days later to determine movements of occupants among tree holes. For comparison, control clusters (i.e. randomly selected clusters where no manipulations were performed) were also visited on two occasions 2–9 days apart. Two additional clusters were added to the 14 control clusters in 1999 because clusters were visited in preparation for a juvenile to be captured, but that juvenile was not removed. The two extra clusters were combined with the rest of the control clusters and revisited in the same manner as the other controls. The time between visits in control clusters was randomly matched to experimental clusters.

Tree holes were classified as unsuitable for red-cockaded woodpeckers if the hole diameter was greater than 7 cm (after Conner et al. 1996). Individuals were believed to have immigrated to the cluster if the number of individuals was greater on the second of two successive surveys. Likewise, an individual was assumed to have emigrated if the number of individuals was fewer on the second of two successive surveys. All other among-tree-hole movements were termed “switches”. Emigration events, immigration events, and switches were collectively referred to as “moves”.

Variables were tested for normality using the Shapiro Wilk's W Test and comparisons among variables were initially investigated using Spearman rank correlations. I used logistic regression to examine the effect of intersurvey interval on likelihood the focal tree hole would be occupied or that members of the assemblage would move among tree holes. Candidate variables were used in multiple logistic regression to find the best predictor of focal tree-hole occupancy following removal of the juvenile. I tested movement events between treatments using Pearson χ^2 . Movement data were compared across treatments using the Wilcoxon Signed Ranks test. Likelihood ratios were calculated to compare the interaction between red-cockaded woodpecker and red-bellied woodpecker movement patterns in removal clusters. Candidate variables, based upon correlation analyses, were used in multiple logistic regression to find the best predictors of movement among tree holes in the experimental treatments.

Experiment 2 — Removal of red-bellied woodpeckers

To evaluate the competitive interaction between red-bellied woodpeckers and other members of the species assemblage, red-bellied woodpeckers were removed from their tree holes within 28 experimental clusters from January through April 2001. Removal clusters were visited bimonthly to detect the presence of red-bellied woodpeckers. Using a similar monitoring protocol as was used for the red-cockaded woodpecker removal study (Experiment 1), all tree holes at the site of removal were surveyed on the same night. After 1–6 days all tree holes in the cluster were resurveyed to determine their occupancy. I compared data from 14 control clusters observed during the same time of year, as part of Experiment 3 (see below). Red-bellied woodpeckers were

permanently removed at night as part of several other studies (see Schrader et al. 2003, Walters and James unpub ms, Walters unpub ms). Statistical tests followed methods used in Experiment 1.

Experiment 3 — Occlusion of tree holes

To evaluate the effect of increasing the propensity for the assemblage to interact competitively, the number of tree holes in a cluster was reduced by one by occluding a randomly selected tree hole that contained the species of interest (N = 40 red-cocked woodpecker trials, N = 27 red-bellied woodpecker trials). In this manner, individuals were forced to seek out another tree hole or to roost in the open. The red-bellied woodpecker roost hole occlusion experiment was performed over 5 days in November 1999 and April and September of 2000. The cluster was surveyed at night on day 1 and a piece of 6 mm gauge hardware cloth was tacked over the hole entrance while the bird was away from the hole on day 2. On the night of day 3 all tree holes in the cluster were resurveyed and the hardware cloth was removed. The cluster was surveyed for a final time on day 5. Likewise, the red-cockaded woodpecker roost hole occlusion experiment was performed in November of 1999 and March and September of 2000. Protocol for the experiment was identical (including experimental clusters) to that of the red-bellied woodpecker occlusion experiment.

The experiments were conducted in September and November because I deemed it to be the time of year when competition for tree holes should be most intense (i.e. juvenile woodpeckers should be roosting in tree holes before they disperse from their natal groups). March and early April were chosen because that time of year should yield the least intense competition for tree holes. Many migrant species have not yet returned and all young from the previous year should have dispersed, unless they are red-cockaded woodpeckers that have elected to remain as helpers. I did not conduct occlusion experiments in the breeding season (late April through late July). The timing of the experiments, however, allowed us to test the interactions among resident species by occluding the two most numerically abundant species in the absence of migratory

species. Statistical tests followed methods used in Experiment 1. All statistical tests were conducted using SPSS (SPSS Inc. 2000).

Results

Experiment 1 — Removal of juvenile red-cockaded woodpeckers

Focal tree-hole occupancy

Empty tree holes were re-occupied about 30% of the time (Table 1). It was equally likely that the occupant would be a red-cockaded woodpecker or a red-bellied woodpecker. The red-cockaded woodpeckers that eventually occupied the focal tree hole switched tree holes from within the cluster (Table 2a, 52.6% probability of the hole being occupied if a red-cockaded woodpecker moves within the cluster) whereas when a red-bellied woodpecker occupied the empty, it immigrated into the cluster (52.7% probability of focal hole being occupied if a red-bellied woodpecker immigrates into the site).

Movements among the assemblage

Overall movements of red-cockaded and red-bellied woodpeckers among tree holes were greater at clusters where juvenile red-cockaded woodpeckers had been removed (Pearson $\chi^2 = 3.469$, $p = 0.063$; Pearson $\chi^2 = 6.523$, $p = 0.011$, respectively; $n = 47$) than in control clusters ($n = 30$). Within removal clusters, red-cockaded woodpeckers and red-bellied woodpeckers were similar in their propensity to move ($Z = -1.126$, $p = 0.260$). Within control clusters, movements were identical between species. I did not find evidence of an interaction between red-cockaded woodpecker overall movement and red-bellied woodpecker overall movement in removal clusters (Likelihood Ratio, $p = 0.840$). In the red-cockaded woodpecker removal experiment, the best predictors of movement among the assemblage were the number of suitable unoccupied tree holes at the time the juvenile red-cockaded woodpecker was removed and whether an

Table 1. Outcome of focal tree hole where red-cockaded or red-bellied woodpecker was removed.

Species removed	Outcome		
	Empty	Red-cockaded woodpecker	Red-bellied woodpecker
Red-cockaded woodpecker	34	7	6
Red-bellied woodpecker	40	11	6

$\chi^2 = 0.418, p = 0.812$

Table 2. Logistic regression tables.

Variable	β	Standard error	<i>P</i>	Odds ratio
(a) Occupation of focal tree hole following removal of a juvenile red-cockaded woodpecker				
Intercept	-2.727	0.733	0.000	0.065
Red-bellied woodpecker immigrates	2.835	1.162	0.015	17.023
Any movement by a red-cockaded woodpecker	2.830	0.944	0.003	16.939
(b) Movement among holes within a cluster following the removal of a juvenile red-cockaded woodpecker.				
Intercept	-0.443	0.380	0.244	0.642
Treatment	-2.406	0.702	0.001	0.090
Suitable unoccupied tree holes	0.6480	0.272	0.017	1.911
(c) The relationship between the number of suitable unoccupied tree holes and movement (i.e. any change in tree-hole occupancy, excluding occluded individuals that roosted outside of a tree hole) among all members of the assemblage in control (i) and occlusion (ii) clusters.				
(i) Intercept	-2.378	0.562	0.000	0.093
Suitable unoccupied tree hole	0.642	0.219	0.003	1.901
(ii) Intercept	-0.731	0.491	0.137	0.482
Suitable unoccupied tree hole	0.516	0.226	0.022	1.675

individual was removed or not (control vs removal, Table 2b). The probability of moving increases with the number of unoccupied suitable tree holes (Figure 1).

Intersurvey interval

The intersurvey interval varied from 2 to 9 days ($\bar{X} = 3.50 \pm 1.76$ SD) for control clusters and 2–8 days ($\bar{X} = 3.51 \pm 1.79$ SD) for juvenile removal clusters. In order to determine whether my results were biased by the variation in my post-removal survey interval (i.e. one might expect that the greater the interval the more likely the vacated tree hole would be occupied), I tested for the effect of interval length. Focal tree holes (i.e. the hole that the juvenile was removed from) were not more likely to be occupied during longer intersurvey intervals (logistic regression, $p = 0.764$), nor were occupants more likely to move among tree holes as intersurvey interval increased (logistic regression: control, $p = 0.673$; removal, $p = 0.771$). In other words, tree-hole occupants respond to the removal of the juvenile within 48 hours and are not more likely to switch tree holes if more time is allowed.

Experiment 2 — Removal of red-bellied woodpeckers

Empty tree holes were re-occupied about 30% of the time (Table 1). It was twice as likely that the occupant would be a red-cockaded woodpecker than a red-bellied woodpecker following the removal of a red-bellied woodpecker. In control clusters, there were only 2 moves (0.07 per cluster) of red-cockaded or red-bellied woodpeckers observed between surveys ($n = 28$ surveys). In clusters where red-bellied woodpeckers were removed, however, there were nearly 4 times as many movements per cluster for red-cockaded woodpeckers (0.25 per cluster) and twice as many for red-bellied woodpeckers (0.13 per cluster, $n = 48$ surveys).

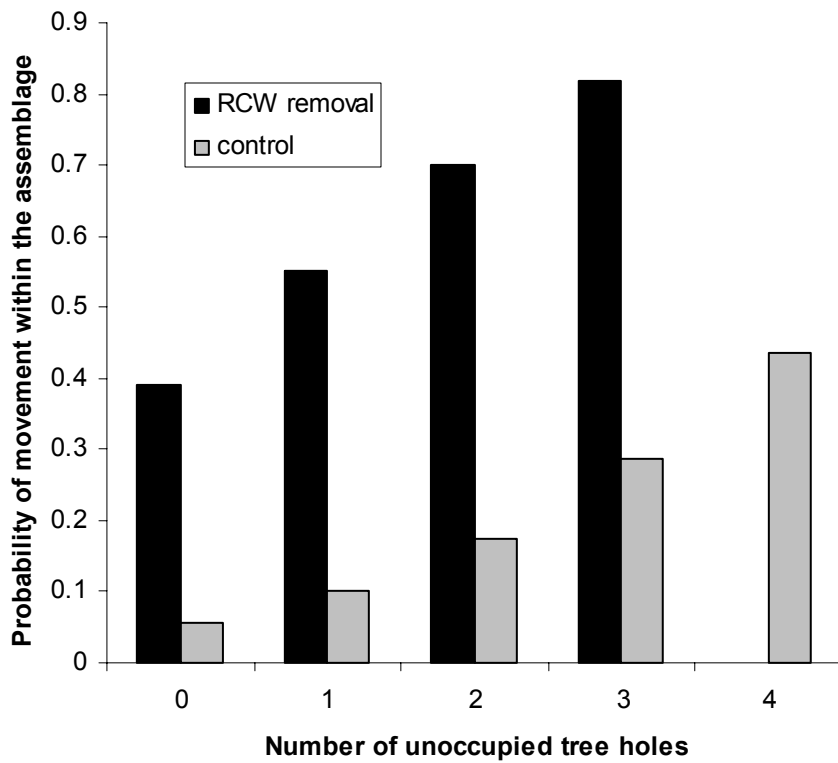


Figure 1. The probability of members of the assemblage moving as a function of the number of suitable unoccupied tree holes by treatment type. Only observed ranges are shown. RCW = Red-cockaded woodpecker

Comparison of Experiment 1 vs Experiment 2

There was no difference in the subsequent occupancy of focal tree holes where red-cockaded woodpeckers or red-bellied woodpeckers were removed (Table 1, Pearson $\chi^2 = 0.418$, $p = 0.812$). There was, however, more movement among the assemblage (i.e. among all tree holes) in clusters where red-cockaded woodpeckers were removed than in clusters where red-bellied woodpeckers were removed (Table 3, Pearson $\chi^2 = 6.169$, $p = 0.013$). If we, however, control for the fact that the categories for red-bellied woodpecker switches and emigration are not applicable because I removed all red-bellied woodpeckers (Table 4), I find that overall movements do not differ between the treatments (Pearson $\chi^2 = 0.558$, $p = 0.455$).

Intersurvey interval

The number of intersurvey days between initial survey (i.e. the night the woodpecker was removed) and final survey ranged from 1 to 6 days ($n = 48$, median = 4.0). The control ranged from 1 to 3 days ($n = 28$, median = 1.5). As I found in the red-cockaded woodpecker removal experiment, there was no effect of the intersurvey interval on the propensity of the focal tree hole to attract an occupant (logistic regression: $p = 0.100$). There was also no effect of the number of days on the likelihood of tree-hole occupants to move among tree holes (logistic regression: removal, $p = 0.192$; control, $p = 0.917$).

Experiment 3 — Occlusion of tree holes

When holes used by red-cockaded woodpeckers ($n = 40$) and red-bellied woodpeckers ($n = 27$) were occluded, proportionally nearly 2.5 times more red-bellied woodpeckers switched to another available tree hole than red-cockaded woodpeckers (Table 5). I did not record any case of a red-cockaded woodpecker displacing a red-bellied woodpecker or vice versa, following occlusion of either species. When I examined the movements associated with avian and mammalian members of the assemblage, there were no differences between red-cockaded woodpecker occluded

Table 3. Movements among tree holes by avian and mammalian members of the assemblage following removal of a red-cockaded woodpecker or a red-bellied woodpecker.

Species Removed	Movement	
	Move	No Move
RCW	25	22
RBW	17	41

Pearson $\chi^2 = 6.169$, $p = 0.013$

Table 4. Nature of movements in cluster where either a red-cockaded or red-bellied woodpecker was removed.

Species removed	Outcome					
	Red-cockaded woodpecker			Red-bellied woodpecker		
	Switch	Immigration	Emigration	Switch	Immigration	Emigration
Red-cockaded woodpecker	6	4	4	5	11	4
Red-bellied woodpecker	3	8	1	N/A	6	N/A

Switch: individual switches from one known tree hole to another

Immigration: individual immigrates into cluster, not having previously been observed using a tree hole in the cluster

Emigration: individual emigrates from the cluster

NA: no red-bellied woodpeckers were present to switch or to emigrate because they had been removed

Table 5. The fate of the focal individual following the occlusion of its tree hole.

Species	Outcome	
	Roosted Out	Switched Tree Holes
Red-cockaded woodpecker	35	5
Red-bellied woodpecker	19	8

Pearson $\chi^2 = 3.025$, $p = 0.082$

sites and associated control sites (Pearson $\chi^2 = 1.210$, $p = 0.271$) but there was more movement in the red-bellied woodpecker occlusion sites when compared with controls (Pearson $\chi^2 = 6.355$, $p = 0.012$, Table 6). If I focus solely on the movements of red-cockaded and red-bellied woodpeckers, both species exhibited greater movements in occlusion sites relative to controls (Table 7).

The probability of movement increases with the number of unoccupied tree holes for each treatment (Figure 2). In control clusters, given that there is one unoccupied suitable tree hole available, there is a 15.0% probability that movement among the species assemblage will ensue. There is nearly three times (44.7%) the probability of the same movement when an occupant is occluded (Table 2c). A variety of species were involved in the movement events in control clusters but movements were largely confined to red-cockaded woodpeckers, red-bellied woodpeckers, and southern flying squirrels in occlusion clusters (Figure 3).

Discussion

My experiments provide support for the existence of competition for roost holes for red-cockaded woodpeckers and red-bellied woodpeckers. Interactions within and between the two species appear to be taking place over periods as short as 24 hrs (i.e. empty tree holes tend to be re-occupied soon after a bird is removed). The fact that the intersurvey interval did not affect the focal tree hole's receipt of new occupants in either the red-cockaded woodpecker or red-bellied woodpecker removal experiments suggests that both species are aware of the pattern of occupancy of all the tree holes within the cluster. Because some tree holes were reoccupied in as little as 24 hrs, it suggests that individuals frequently monitor suitable tree holes within their territories (Ligon 1971).

If red-bellied woodpeckers are dominant over red-cockaded woodpeckers (i.e., "cavity kleptoparasites", *sensu* Kappes 1997), they should be replaced by red-cockaded woodpeckers when the former are removed. If red-cockaded woodpeckers are

Table 6. Movements among tree holes by avian and mammalian members of the assemblage following occlusion of focal tree hole.

(a) Red-cockaded woodpecker occluded

Treatment	Movement	
	Move	No Move
occlusion	15	25
control	11	31

Pearson $\chi^2 = 1.210$, $p = 0.271$

(b) Red-bellied woodpecker occluded

Treatment	Movement	
	Move	No Move
occlusion	12	15
control	7	35

Pearson $\chi^2 = 6.355$, $p = 0.012$

Table 7. Movements among tree holes by red-cockaded and red-bellied woodpeckers following occlusion of focal tree hole.

(a) Red-cockaded woodpecker occluded

Treatment	Movement	
	Move	No Move
occlusion	13	27
control	6	36

Pearson $\chi^2 = 3.818$, $p = 0.051$

(b) Red-bellied woodpecker occluded

Treatment	Movement	
	Move	No Move
occlusion	12	15
control	5	37

Pearson $\chi^2 = 9.372$, $p = 0.002$

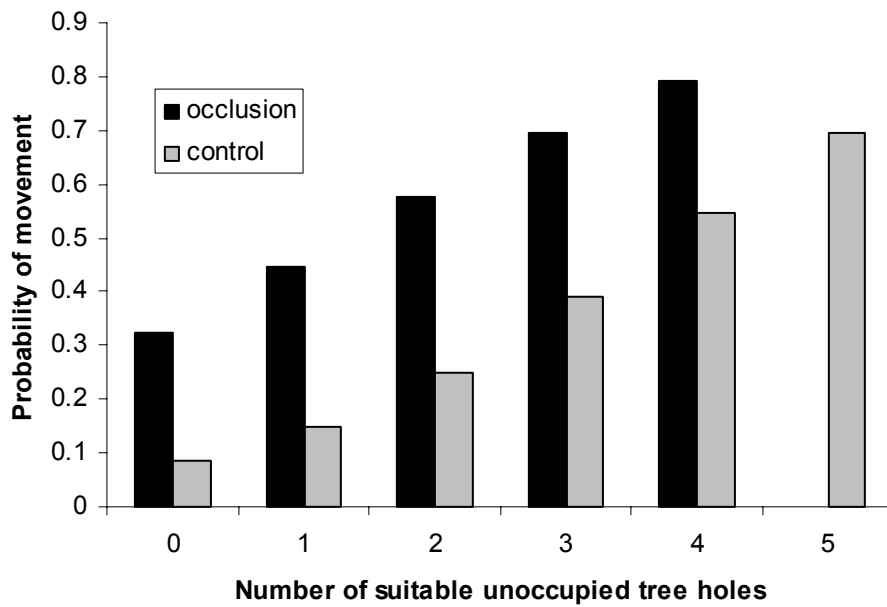
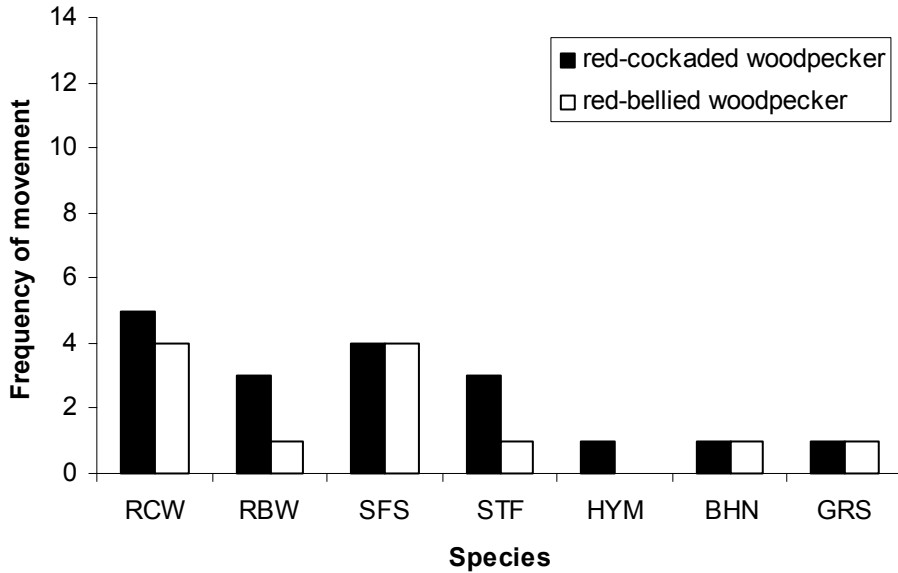


Figure 2. The probability of members of the assemblage moving (any change in tree-hole occupancy, excluding occluded individuals that roosted outside of a tree hole) following the occlusion of either a red-bellied woodpecker or a red-cockaded woodpecker, as a function of the number of suitable unoccupied tree holes by treatment type. Only observed ranges are shown.

a) Control treatments (RCW: n = 42, RBW: n = 41)



b) Occlusion treatments (RCW: n = 40, RBW: n = 27)

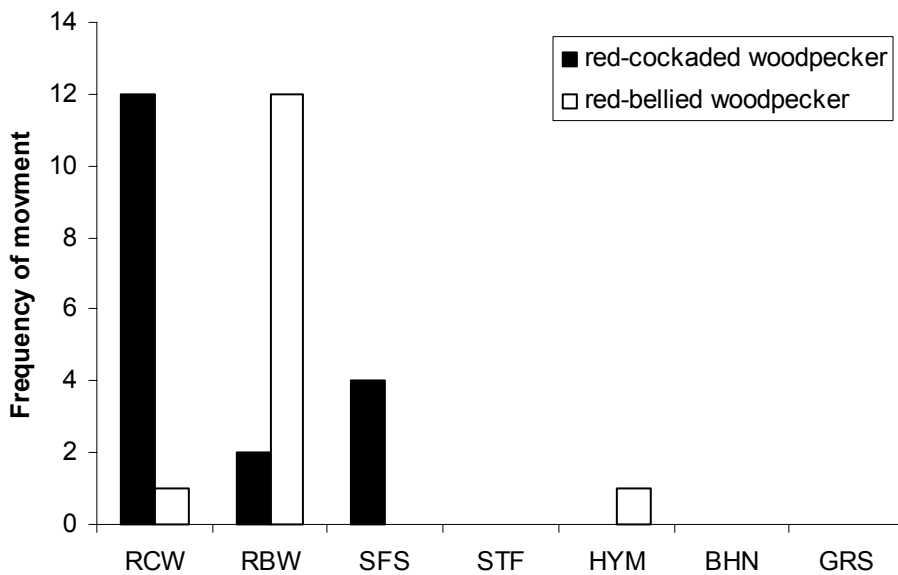


Figure 3. Members of the species assemblage that moved (i.e. any change in tree-hole occupancy, excluding occluded individuals that roosted outside of a tree hole) during the occlusion study. RCW: red-cockaded woodpecker, RBW: red-bellied woodpecker, SFS: southern flying squirrel, STF: squirrel tree frog, HYM: hymenopteran species, BHN: brown-headed nuthatch, GRS: gray rat snake

dominant over red-bellied woodpeckers, then when red-cockaded woodpeckers are removed from their tree holes, red-bellied woodpeckers should replace them, ignoring any effects attributable to dominance hierarchies within species. Because I observed red-cockaded woodpeckers occupying tree holes where red-bellied woodpeckers had been removed and vice versa, I conclude that the relationship between the two species is competitive (Hodge and Arthur 1996). That is, each species is negatively affected by the other.

My results do not support the interpretation by Kappes (1997) that the relationship is contramensal (*sensu* Hodge and Arthur). He argues that because red-cockaded woodpeckers make all of the tree holes that red-bellied woodpeckers use, that the relationship is “kleptoparasitic”, positive for the red-bellied woodpeckers and negative for the red-cockaded woodpeckers. However, at the level of the individual, a red-bellied woodpecker that has been excluded from a tree hole by a red-cockaded woodpecker is experiencing a negative interaction. Kappes compares individual-level effects without considering temporal scale. He argues, on the one hand, that at the species level red-cockaded woodpeckers create the tree holes but on the other hand that red-bellied woodpeckers and red-cockaded woodpeckers interact at the level of the individual. It is true that red-cockaded woodpeckers create the tree holes but not all individuals created the hole that they are using (Baker 1971). Research in other populations has shown that in the majority of family groups only one individual was involved in excavation of tree holes (Harding 1997). Previous research has shown that tree holes can require the entire lifespan (\approx generation time) of an individual to complete (i.e. 5 years, USFWS 2003) and, in fact, can take up to two or more generations to complete (Conner and Rudolph 1995a, Harding 1997). Likewise, some tree holes have been used by red-cockaded woodpeckers for 20 (Lay and Russell 1970) and even 30 years (Conner and Rudolph 1995a). It follows, thus, that if (a) the length of time to create a tree hole can exceed the average red-cockaded woodpecker generation time, (b) only one member of the family group is contributing to tree-hole excavation, and (c) family groups are not stable over time (Lennartz et al. 1987); then most red-cockaded woodpeckers and red-

bellied woodpeckers are using tree holes that neither individual created. Therefore, one cannot assume the relationship is negative for an individual red-cockaded woodpecker without knowing whether that individual created the tree hole.

Both red-cockaded woodpeckers and red-bellied woodpeckers use exploitative (i.e. they arrive at and enter a tree hole before their competitor reaches it) and, to a lesser extent, interference competition to obtain tree holes (Ligon 1971, pers. obs.). In my population, because movements in clusters where red-bellied woodpeckers were removed were not statistically different from those in control clusters, red-bellied woodpeckers are not competitively dominant to red-cockaded woodpeckers. Otherwise, I would have found red-cockaded woodpeckers moving to the tree holes from which the red-bellied woodpeckers were removed. In fact, I did not find any differences in the outcomes of vacated tree holes regardless of species removed. By removing *all* red-bellied woodpeckers in the cluster, I attempted to maximize the opportunities for red-cockaded woodpeckers to move to a more suitable tree hole. My findings are further supported by Neal et al. (1992) in a previous study where red-bellied woodpeckers, a species that is slightly larger than a red-cockaded woodpecker, were prevented from re-occupying known roost holes by the placement of a device that restricted the entrance hole diameter (Carter et al. 1989).

Contrary to expectation, not all holes were re-occupied by red-cockaded woodpeckers. In my study, there was actually more movement (or the same movement, depending upon whether one controls for the fact that all red-bellied woodpeckers were removed) in clusters where red-cockaded woodpeckers were removed than where red-bellied woodpeckers were removed. One would expect there to be more movement when the dominant species is removed (i.e. the subordinate species is released from competitive interactions), especially considering removal of all red-bellied woodpeckers in the cluster. Perhaps red-bellied woodpeckers are occupying tree holes that are not favoured by red-cockaded woodpeckers. If so, then either red-cockaded woodpeckers are marginalizing the red-bellied woodpeckers or that they coexist with slightly different tree-hole requirements (i.e. resource partitioning, Schoener

1974a). Neither conclusion supports red-bellied woodpeckers being dominant to red-cockaded woodpeckers, as has been reported for other populations.

Interestingly, when juvenile red-cockaded woodpeckers were removed from tree holes, the best predictors of eventual occupancy were immigrating red-bellied woodpeckers or red-cockaded woodpeckers moving from within or among clusters. I did not find that red-bellied woodpeckers were moving from within the cluster to the vacated tree hole. Behaviorally, immigrating red-bellied woodpeckers may be more likely to investigate potential roosting holes than are resident red-bellied woodpeckers. The frequency with which immigrating birds were discovered also suggests a remarkable “floater” population (Zack and Stutchbury 1992). It appears that many individual red-bellied woodpeckers are continually exploring potential roost sites.

The increased probability of movement associated with the number of available suitable tree holes seems to be counterintuitive. One might expect increased competitive interactions and more movement when there are fewer tree holes available. But, movement among tree holes was more likely when there were vacant tree holes for individuals to move to. My observations are that it is unusual for individuals to be usurped from tree holes. As such, prospecting individuals are more likely to occupy an unoccupied tree hole than they are to usurp another individual.

The fact that occluding red-cockaded woodpeckers' roost holes did not cause more movement (defined as any change in tree-hole occupancy) than occurred in control clusters reveals that red-cockaded woodpeckers are reluctant to move from their tree holes. Red-bellied woodpeckers, on the other hand, did move under these circumstances. Red-cockaded woodpeckers must maintain resin wells whereas red-bellied woodpeckers are less dependent on tree characteristics. When the roost holes of transient (or extraterritorial, Hooper and Lennartz 1983) red-cockaded woodpeckers (i.e. those individuals found temporarily roosting in the experimental cluster, that were not part of that cluster's social group) were occluded, the birds were unlikely to return to the tree holes from which they were barred. The more an individual has invested in a tree hole (whether it made the hole or whether it has been maintaining the resin wells

for a period of time), the more likely it is to (a) return to that tree hole following the removal of the occlusion, and (b) it is to roost out on the side of a tree, rather than using an alternative tree hole.

For competition to be present among members of the species assemblage, suitable tree holes must be limiting. Adding artificial tree holes to existing populations of red-cockaded woodpeckers induces new social groups to be created, suggesting that tree-hole availability is limiting population size (Copeyon et al. 1991, Walters et al. 1992). Of particular note in my study was the finding that over 70% of the tree holes, from which woodpeckers were removed, remained empty. One might conclude that the holes remained empty because individuals were being removed from unsuitable tree holes. Only one tree hole, however, in each of the removal treatments had an entrance diameter greater than 7 cm (i.e. unsuitable) so tree-hole quality is unlikely to be a satisfactory explanation. Individual red-cockaded woodpeckers are known to engage in extraterritorial roosting behavior when insufficient numbers of suitable tree holes are available (Hooper and Lennartz 1983). My work, in addition to others (e.g. Walters et al. 1992), has shown that birds will often roost in the open as a response to interspecific competition (i.e. a competitor usurps the tree hole, Kappes and Harris 1995, Kappes 1997). Adult red-cockaded woodpeckers will sometimes roost outside of tree holes when the tree dies or is otherwise unsuitable (Hooper 1983, Hooper and Lennartz 1983, Walters and Kneitel 2004). Clearly, it is the number of *suitable* tree holes that is important as opposed to overall abundance of tree holes. The risk of mortality associated with roosting in a dead tree (i.e. increased risk of predation by arboreal snakes) may outweigh the associated risk of roosting outside of a tree hole (Ligon 1970).

From a conservation perspective, my study shows that removal of juvenile red-cockaded woodpeckers for translocation may have negative effects on the resident family group. I have documented differences that occur between control clusters and those used to remove juvenile red-cockaded woodpeckers for relocation to other populations, as part of the overall recovery plan for the species. When juvenile red-

cockaded woodpeckers are removed, their absence affects the short-term turnover of organisms using tree holes. Longer-term studies will be needed to measure the effect of these interactions on the respective populations. If remaining members of red-cockaded woodpecker family groups are being negatively affected by the removal of the juveniles, managers responsible for the recovery of the species will need to evaluate the negative effects of removing juveniles on the donor population against the positive effects of augmenting smaller populations. A paradox appears to exist in the sense that more tree holes are available for red-cockaded woodpecker family groups once the juvenile is removed (i.e. a good thing if tree holes are limiting) yet family groups are reduced such that they may not be as effective at defending the tree holes in the cluster from competitors (Jackson 1978). My observations suggest that, by creating open tree holes, this disrupts the “balance” that may exist among territorial species that will collectively defend the cluster from conspecific individuals.

My estimates of movement are conservative because I did not discriminate among conspecific individuals, due to the limits of the infrared inspection device. It is also possible that my estimates of intraspecific competition, or dominance hierarchy, are also conservative. Thus, any detectable effects among the assemblage because of my manipulations should be viewed as conservative measures.

A further avenue of investigation is the role of group dynamics in defending tree holes from competitors (Beckett 1971). I have witnessed, for example, many occasions where the family group of red-cockaded woodpeckers defended its territory from unrelated conspecific individuals who ventured within the cluster in search of a tree hole. My impression is that larger groups are more likely to observe these extraterritorial birds and exclude them from using tree holes. It is unclear whether my finding that less red-cockaded woodpeckers move into clusters when group size is large because the larger group observes and repels immigrating individuals or whether it means that there are fewer individuals roosting extraterritorially when more tree holes are available within the group’s cluster. Assuming the former argument, by permanently removing occupants from within their defended territory, opportunities for dispersing

birds to “invade” these territories may be increased. Thus, defence and competitive interactions may be a property of the overall group size of each species. In fact, Jackson (1978) suggested that the clustering of tree holes by red-cockaded woodpecker social groups may be adaptive in reducing competition for tree holes in environments where tree holes are limiting.

By examining how individuals compete for tree holes, I have provided the competitive mechanisms that may exist in the assemblage. It is important to note that I have established that the two most numerous species in the species assemblage are competitors. That is, each species is equally likely to displace the other and does not support the contention that the interaction is one way (i.e. that red-cockaded woodpeckers are never able to successfully defend their tree holes from red-bellied woodpeckers; Ligon 1970, Jackson 1978, Kappes 1997). My next step is to evaluate the population-level effects of the interactions among individuals and, thus, link short-term behavioral interactions with longer-term population-level effects. I also need to study interactions among the species that are less numerically dominant (e.g. pileated woodpeckers) or seasonal in their occurrence (e.g. eastern bluebirds), for these species may exert proportionally larger effects on the assemblage than I might predict (Abrams 1987) or indirect interactions that may not be readily apparent (Miller and Kerfoot 1987). Only after all species in the assemblage are considered can one fully appreciate the range and nature of interactions.

I began this discussion by examining the recent focus on trait-mediated interactions and the importance of individual behavior in predicting population-level outcomes. This study has shown that individuals do not all behave in a similar manner. Some individuals were willing to switch tree holes when occluded while others were not. In a similar fashion, some red-cockaded woodpeckers were dominant to red-bellied woodpeckers while some were not. Given the variability in individual behavior, researchers must exercise caution when reporting anecdotal observations without experimental support. Eventually, as has been argued elsewhere (e.g. Łomnicki 1988,

Sutherland 1996), understanding the scope of individual behavior will allow for one to relate mechanisms to population outcomes.

2. INTERACTIONS BETWEEN TWO SPECIES OF WOODPECKERS: A COMPARISON OF INDIVIDUAL BEHAVIOR AND POPULATION-LEVEL RESPONSES

Introduction

The measurement of the interaction among species in a community is typically framed in terms of a community matrix (Laska and Wootton 1998). Depending upon the type of matrix, investigators are usually interested in (a) the pairwise population-level effect of one species on another, derived from Lotka-Volterra models (MacArthur 1972, Abrams 1987), or (b) in the *per capita* effect of one species on another (Laska and Wootton 1998). The *per capita* effect is important because it is at the level of the individual that interactions take place (Levins 1968, Schoener 1974a, Martin 1986, Tilman 1987, Łomnicki 1988). Reviews of competition studies (e.g. Connell 1983, Schoener 1983, Sih et al. 1985, Goldberg and Barton 1992, Gurevitch et al. 1992) show, however, that they rarely address mechanisms of competition at the individual level. Another approach is to model explicit resource interactions (e.g. Tilman 1982, Chase and Leibold 2003), providing a framework for understanding how species interact based upon resource use. A third approach is to attempt to link individual behavior with population-level outcomes (e.g. Werner 1992, Werner and Anholt 1996, Beckerman et al. 1997, Relyea and Yurewicz 2002).

I conducted field experiments with two species of woodpeckers, the red-cockaded woodpecker (*Picoides borealis*) and the red-bellied woodpecker (*Melanerpes carolinus*) to determine whether behavioral interactions at individual levels manifest themselves at population levels. The removal experiment that I present was designed to examine the nature of interspecific interactions by providing direct tests of specific hypotheses about

resource use (Connell 1975). When one competitor was removed, I asked whether there was an increase in fitness in the other competitor. I compare the findings of a sustained removal experiment with previous findings about short-term individual behavior (Walters and James unpub ms).

My model system is based upon competition for a limiting discrete resource, nest and roost holes in living longleaf pine trees (*Pinus palustris*). The tree holes are created by the endangered keystone species, the red-cockaded woodpecker (USFWS 2003). Typically, a family of red-cockaded woodpeckers roosts in individual tree holes that have been excavated by their ancestors (Conner and Rudolph 1995a, Harding 1997). Over time, tree holes accumulate in the cluster of trees in the center of a territory (Walters et al. 1988). A suite of additional species is attracted to these tree holes for roosting and nesting (Conner et al. 1997, Walters and Kneitel 2004). Besides red-cockaded woodpeckers, vertebrate species that use the tree holes for reproduction include other birds (red-bellied woodpeckers, eastern bluebirds [*Sialia sialis*], great crested flycatchers [*Myarchus crinitis*], eastern screech owl [*Otus asio*]), and mammals (southern flying squirrel [*Glaucomys volans*]). Other vertebrate species that use the tree holes for roosting, but not reproduction, include tree frogs (*Hyla* sp.), skinks (*Eumeces* sp.), and snakes (*Elaphe* sp., Rudolph et al. 1990, Conner et al. 1997).

The red-cockaded woodpecker occurs mostly in stands of naturally regenerated open pine woods that are managed by frequent prescribed burning and thinning (James et al. 1997, James et al. 2001). The species has declined over most of its geographic range due primarily to habitat loss and fragmentation (Conner et al. 2001). As their populations have declined, additional factors associated with small population sizes may be accelerating declines such that extinction is imminent. My goal was to examine the role that potentially competing members of the species assemblage may be playing in the decline of red-cockaded woodpeckers. In my study area in the Apalachicola National Forest in northern Florida, red-bellied woodpeckers are the most abundant potential competitor.

Red-bellied woodpeckers, like red-cockaded woodpeckers, are primary tree-hole nesters. They are found in many habitats in eastern North America (Shackelford et al. 2000). In areas of the southeastern United States where red-bellied and red-cockaded woodpeckers co-occur, red-bellied woodpeckers apparently prefer to use red-cockaded woodpecker tree holes rather than excavate their own in dead trees. Past observations of individual behavior have suggested that red-bellied woodpeckers are strong competitors for red-cockaded woodpecker tree holes (e.g. Ligon 1971, Kappes and Harris 1995, Kappes 1997). However, my previous experimental work examining short-term behavioral interactions between the two species (Walters and James unpub ms) shows that when individuals of either species were removed from tree holes, many holes remained unoccupied for several days. When tree holes were re-occupied, it was equally likely that the new occupant would be the same or the other species. I also showed that red-cockaded woodpeckers are reluctant to move among tree holes, presumably due to their large investment in maintenance of resin wells around their tree holes (Rudolph et al. 1990). Red-bellied woodpeckers, when forced to vacate their preferred tree hole, would often move to other available tree holes within the cluster of trees in the center of a red-cockaded woodpecker territory. Overall, my short-term experiments showed that competitive interactions were surprisingly balanced and refuted the idea that interactions are always negative for red-cockaded woodpeckers and positive for red-bellied woodpeckers (*cf.* Kappes 1997).

My first objective in this study was to determine whether competition between red-bellied woodpeckers and red-cockaded woodpeckers was negatively affecting red-cockaded woodpeckers at the population level. My second objective was to compare my findings based on short-term behavioral interactions at the level of the individual with long-term interactions at the level of the population.

Materials and methods

I conducted experiments in the Apalachicola National Forest in northern Florida (USA). This 228,865 ha forest is divided into two management units, a western

(Apalachicola Ranger District [ARD], 116,999 ha) and an eastern one (Wakulla Ranger District [WRD], 111 866 ha). As a whole, the forest supports 17% of all remaining red-cockaded woodpeckers (USFWS 2003). The ARD supports an estimated 486 family groups and the population appears to be stable while the WRD supports an estimated 138 family groups (USFWS 2003). The latter population is estimated to have declined by 20% in the past 5 years (USFS results).

The experiment employed a split-plot design. Fourteen management compartments ($\bar{X} = 1,292$ ha) were randomly selected from 57 compartments in the ARD that contained at least three red-cockaded family groups (Table 8). Within each compartment, I randomly assigned one of the clusters to a control set, one to a bimonthly removal treatment (sequential pulse experiment), and one to a weekly removal treatment (press experiment, *sensu* Bender et al. 1984) and I monitored the woodpecker groups associated with each cluster from June 1999 until April 2001. In addition, eleven management compartments ($\bar{X} = 1,099$ ha) were randomly selected from among 28 compartments in the WRD that contained at least two red-cockaded family groups and had been monitored since 1992. Within each of 11 compartments I randomly assigned one of the clusters to a control set and one to a bimonthly removal treatment and monitored woodpecker groups associated with each cluster from March 1997 until March 2001. Red-bellied woodpeckers were permanently removed bimonthly from removal clusters by visiting the clusters at night and removing birds from tree holes in which they were roosting. I initially tried to relocate removed individuals but I found that even those that were moved >30 km returned within a few days. Red-bellied woodpeckers were removed from weekly removal clusters by visiting the sites during the day, playing a tape of red-bellied woodpecker vocalizations, and shooting them. All clusters were visited bimonthly and all red-bellied woodpeckers were removed from experimental clusters (bimonthly and weekly treatments) during those visits.

Table 8. Summary of the experimental design used for the red-bellied woodpecker removal experiments, matched within management compartments. Experiments were conducted in the Apalachicola Ranger District (ARD) and the Wakulla Ranger District (WRD).

District	Treatment		Sites (N)		Compartments (N)	Duration
	Bimonthly	Weekly	Control	Removal		
ARD	Yes	Yes	14	14	14	2 years
WRD	Yes	No	11	11	11	4 years

In order to survey sites for tree-hole occupants on bimonthly visits, I determined the number and location of all tree holes (ARD: \bar{X} = 6.55 tree holes per cluster, range = 3—10, N = 42 clusters; WRD \bar{X} = 9.95 tree holes per cluster, range = 6—17, N = 22, Table 9). I monitored all red-cockaded woodpecker groups during the nesting period in order to determine group size, clutch size, and number of fledglings produced each year. For other species I recorded their individual presence in tree holes. Tree-hole occupants were surveyed at night from the ground by shining a flashlight towards the tree-hole entrance and observing occupants that peered out. If no occupants were apparent using this method, an infrared camera mounted on the end of a 15-m telescoping fiberglass pole (Furhman Diversified, Inc.; Seabrook, Texas, USA) was inserted into the tree hole.

I used non-parametric tests (Friedman and Kruskal-Wallis) to compare mean adult group size, mean clutch size, and mean fledgling number of red-cockaded woodpeckers between control sites and bimonthly removal sites. Proportions of successful nests by district, treatment, and year were analyzed using χ^2 . The numbers of roosting red-bellied woodpeckers were compared using the Kruskal-Wallis test. Repeated measures ANOVA was used to compare the numbers of red-bellied woodpeckers roosting at bimonthly intervals among treatments and districts. Tukey's HSD was used to test for post hoc differences among treatments. The proportion of nest holes that were reused in successive years was compared among treatments and districts using χ^2 . In the WRD, the number of years that a nest tree was used for nesting by treatment in the WRD was compared with a Wilcoxon signed ranks test. The proportion of banded red-cockaded woodpeckers that remained on their breeding site from 1999 to 2000 was tested by fitting a logit loglinear model to the data. All statistical tests were conducted using SPSS (SPSS Inc. 2000).

Results

Prior to initiating the red-bellied woodpecker removal experiment in the ARD, I determined that the numbers of red-bellied woodpeckers in each treatment (control,

Table 9. Number of tree holes (mean \pm standard error) per site by district and treatment. Sample size refers to the number of clusters.

District	Treatment		
	Control	Bimonthly	Weekly
ARD (N=14)	6.93 \pm 0.46	6.43 \pm 0.39	6.29 \pm 0.41
WRD (N=11)	9.45 \pm 0.53	10.45 \pm 1.11	—

bimonthly, weekly) were not statistically different (Kruskal-Wallis, $p = 0.193$). In the WRD, I removed red-bellied woodpeckers bimonthly at the rate of 0.71 birds per site per month (Fig. 4). In the ARD, I removed them at the rate of 0.35 birds (49% less than in the WRD) per site. Also in the ARD, I removed 0.48 birds (37% more) per site per month in weekly removals. The number of red-bellied woodpeckers removed per site increased over time (Fig. 4). I was able to significantly reduce the number of red-bellied woodpeckers in each of my treatments (ARD: repeated measures ANOVA, $p = 0.003$, WRD: $p = 0.021$, Fig. 5) but I was not able to eliminate them. In the ARD, both removal treatments differed from the control (bimonthly: $p = 0.037$, weekly: $p = 0.003$, post hoc Tukey's HSD) but not from each other ($p = 0.578$, Fig. 6). 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 ($p = 0.295$).

Surprisingly, the experimental removal of red-bellied woodpeckers had a significant negative effect on red-cockaded woodpecker group size in the ARD in 1999 (Friedman Test $\chi^2 = 7.032$, $df = 2$, $p = 0.030$, Table 10). There was, however, no other statistically significant effect of red-bellied woodpecker removal on red-cockaded woodpecker group size in other years in the WRD or on clutch size, or on number of young fledged in either management district (Table 10). Linked to my finding of reduced group size in removal sites in 1999, there was a negative effect of red-bellied woodpecker removal in 1999 on the proportion of red-cockaded woodpecker nests that successfully fledged young in both districts (ARD: $\chi^2 = 6.239$, $p = 0.044$, WRD: $\chi^2 = 4.701$, $p = 0.030$, Table 11).

There was no difference in the proportion of nest holes that were reused in two 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 12). Likewise, I did not detect any difference in the number of years that a given nest tree was used between the treatments in the WRD when I compared 1998–2000 with 2001–2003 (Wilcoxon Signed Ranks Test $z = -0.141$, $p = 0.888$).

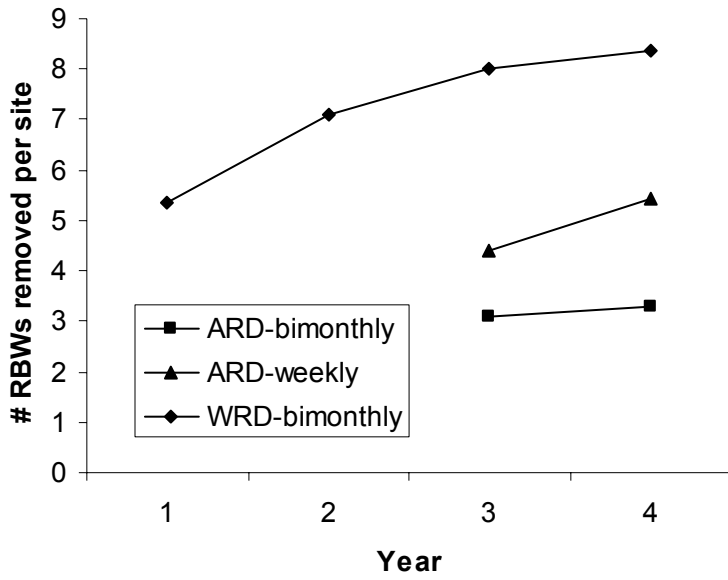


Figure 4. The mean number of red-bellied woodpeckers removed per site by treatment and district. The values for ARD 1999 have been adjusted because removal did not begin until June.

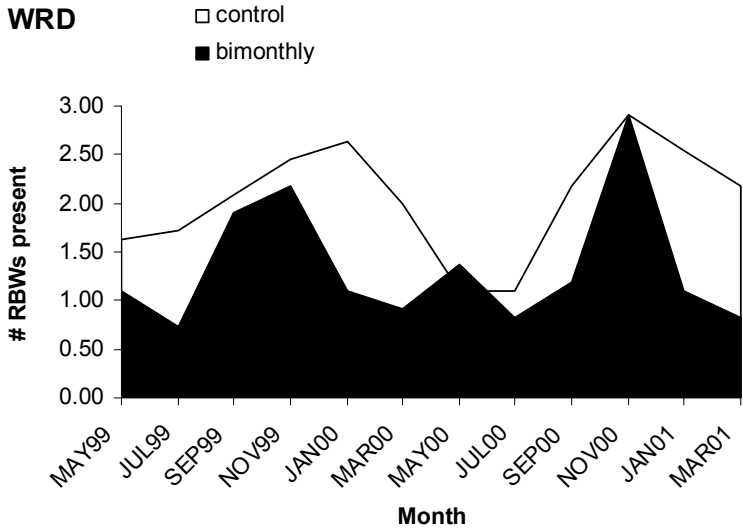
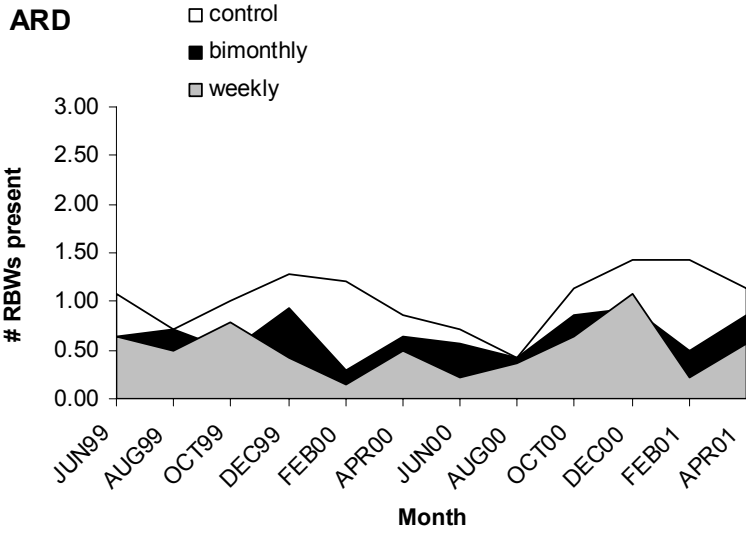


Figure 5. Time series (June 1999–April 2001) of the mean number of red-bellied woodpeckers in control and removal sites for the Apalachicola and Wakulla Ranger Districts.

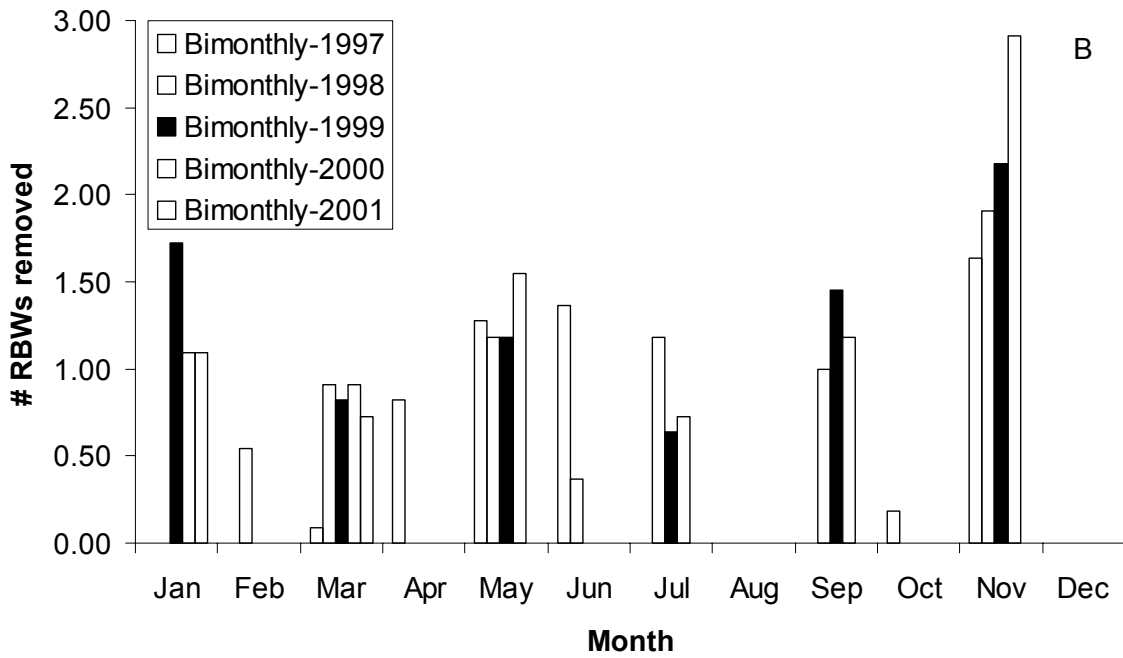
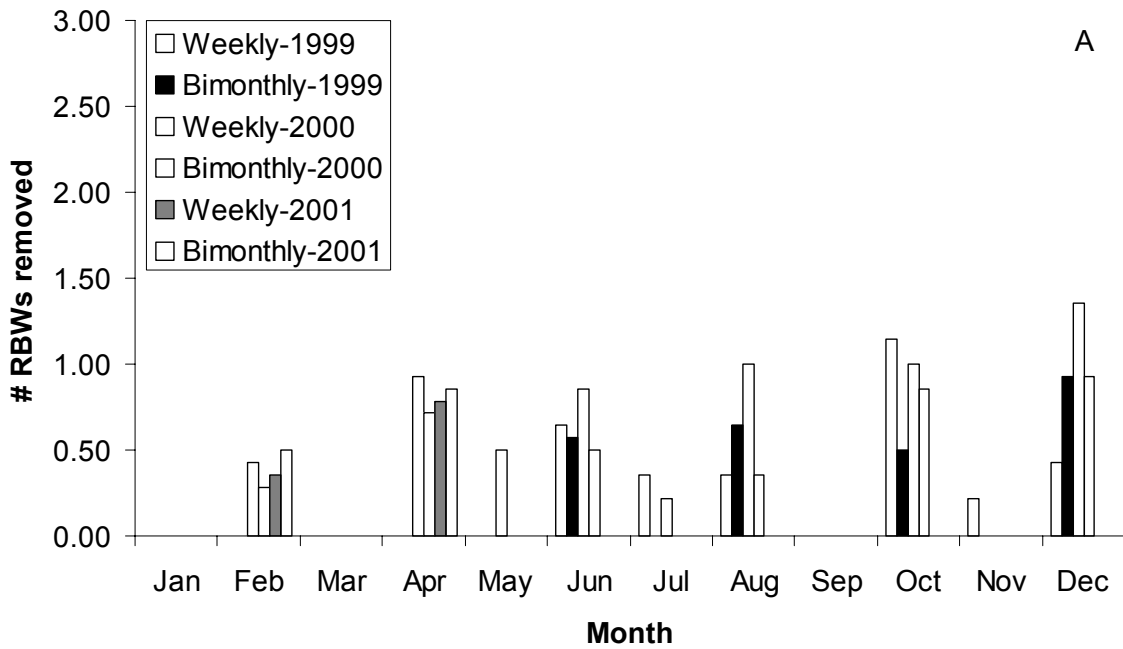


Figure 6. The mean numbers of red-bellied woodpeckers removed per site in the ARD (A) and WRD (B).

Table 10. Summary of red-cockaded woodpecker mean (\pm standard error) productivity measures in the Apalachicola (ARD) and Wakulla (WRD) Ranger Districts (1999–2000).

Productivity Measure	District	Treatment					
		Control		Bimonthly		Weekly	
		1999	2000	1999	2000	1999	2000
Group Size	ARD	2.8 \pm 0.3 ¹	2.4 \pm 0.2	2.4 \pm 0.1 ¹	2.4 \pm 0.1	2.3 \pm 0.1 ¹	2.1 \pm 0.1
	WRD	2.4 \pm 0.2	2.3 \pm 0.2	1.8 \pm 0.3	2.3 \pm 0.1	—	—
Clutch Size	ARD	3.4 \pm 0.2	3.4 \pm 0.2	3.3 \pm 0.1	3.4 \pm 0.2	3.3 \pm 0.2	3.6 \pm 0.3
	WRD	3.4 \pm 0.4	3.1 \pm 0.3	3.3 \pm 0.5	3.5 \pm 0.2	—	—
Fledglings	ARD	2.1 \pm 0.2	2.0 \pm 0.2	2.2 \pm 0.2	2.0 \pm 0.3	1.7 \pm 0.3	1.9 \pm 0.2
	WRD	1.7 \pm 0.2	1.6 \pm 0.2	1.5 \pm 0.3	1.7 \pm 0.2	—	—

¹ Friedman Test $\chi^2 = 7.032$, df = 2, p = 0.030; all other tests non-significant

Table 11. The proportion of successful red-cockaded woodpecker nests by district, year, and district.

District	Year	Treatment			χ^2	P
		Control	Bimonthly	Weekly		
ARD (N=14)	1999	0.93	0.64	0.50	6.239	0.044
	2000	0.79	0.79	0.64	0.985	0.611
WRD (N=11)	1998	0.64	0.45	—	0.733	0.392
	1999	0.82	0.36	—	4.701	0.030
	2000	0.73	0.82	—	0.259	0.611
	2001	0.64	0.73	—	0.210	0.647

Table 12. Proportions of 1999 nest trees reused by red-cockaded woodpeckers in 2000 in the Apalachicola Ranger District (ARD) and the Wakulla Ranger District (WRD). Numbers in parentheses are sample sizes.

District	Experimental Treatment		
	Control	Bimonthly	Weekly
ARD	0.77 (13)	0.67 (12)	0.73 (11)
WRD	0.71 (7)	0.80 (5)	—

ARD: $\chi^2 = 0.329$, $p = 0.848$, WRD: $\chi^2 = 0.114$, $p = 0.735$

I found that the proportion of adult breeding red-cockaded woodpeckers remaining in consecutive years was higher in the ARD (logit likelihood ratio $\chi^2=12.086$, $p=0.034$, Table 13). In my removal treatments in the WRD, both the proportion of males and females decreased, the latter by almost 50%. In contrast, the ARD males seemed unaffected by the removal treatments. Females, on the other hand, in both removal treatments were less likely to remain in a site when red-bellied woodpeckers were removed.

My experiment in the WRD was conducted over 4 years (1997–2001) but the effort in year 1 was not as intensive as in later years (Fig. 6). During the 4 years, the red-cockaded woodpeckers in the removal clusters remained at a lower level than those in the control clusters. Interestingly, variation around the mean was greater in the control groups (Fig. 7A). Red-bellied woodpecker numbers, on the other hand, appeared to follow similar trends to one another in removal and control plots (Fig. 7B). As with my findings for 1999–2001, I found seasonal peaks in spring and fall. Removals made during the winter were quickly replaced but removals made in late spring were not. In control clusters, as red-bellied woodpecker abundances dropped, red-cockaded woodpecker abundances rose, with a lag effect (Fig. 7C).

Discussion

The results of my test of whether red-bellied woodpeckers are exerting population pressure on red-cockaded woodpecker populations are a complex result (Table 14). The results of a previous research study in this forest (Kappes 1997), based primarily upon observations, labeled red-bellied woodpeckers “kleptoparasites” largely because red-cockaded woodpeckers excavate the tree holes that red-bellied woodpeckers subsequently use. Kappes viewed the interaction as asymmetrical (+/-), a term elsewhere labeled *contramensalism* (Hodge and Arthur 1996). His argument is that red-cockaded woodpeckers suffer because red-bellied woodpeckers usurp the tree holes they have created. Red-bellied woodpeckers are said to benefit because they are

Table 13. The proportion of banded red-cockaded woodpeckers that remained at their breeding site from 1999 until 2000 by treatment and district. Numbers in parentheses are sample sizes.

District	Control		Bimonthly		Weekly	
	Male	Female	Male	Female	Male	Female
ARD	0.85 (13)	1.00 (5)	0.91 (11)	0.57 (7)	0.82 (11)	0.60 (5)
WRD	0.78 (9)	0.44 (9)	0.60 (10)	0.20 (10)	—	—

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 $p > 0.100$.

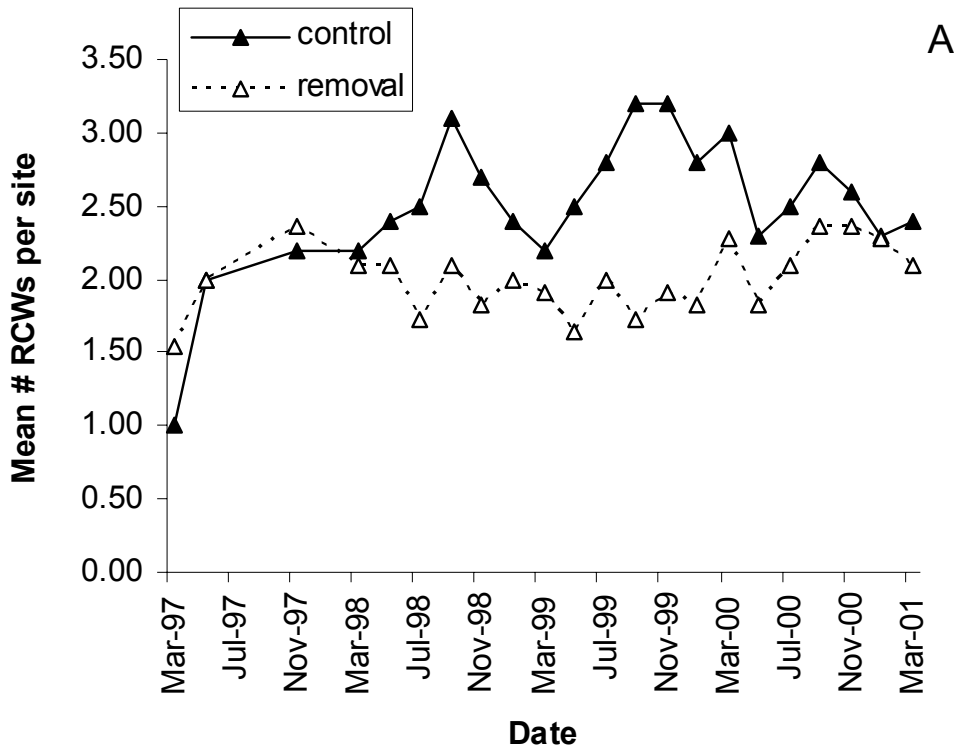


Figure 7A. The mean number of red-cockaded woodpeckers (rcw) per site by treatment in the WRD. N = 10 (control), N = 11 (removal) in the WRD. Data shown spans 4 years (March 1997 to March 2001)

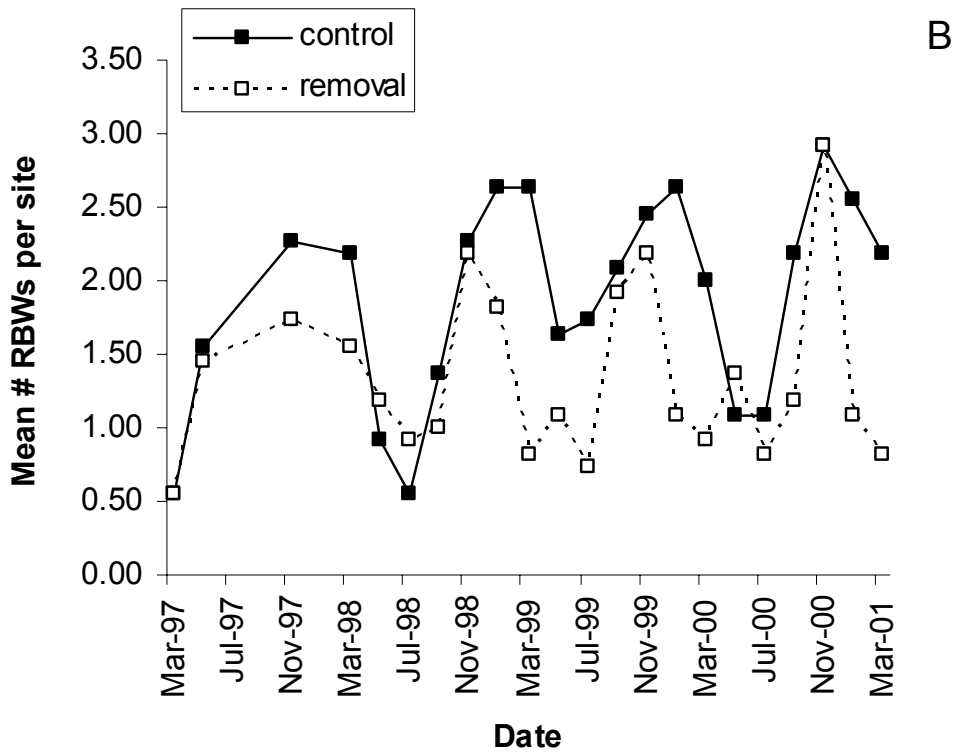


Figure 7B. The mean number of red-bellied woodpeckers (rbw) per site by treatment in the WRD. N = 10 (control), N = 11 (removal) in the WRD. Data shown spans 4 years (March 1997 to March 2001)

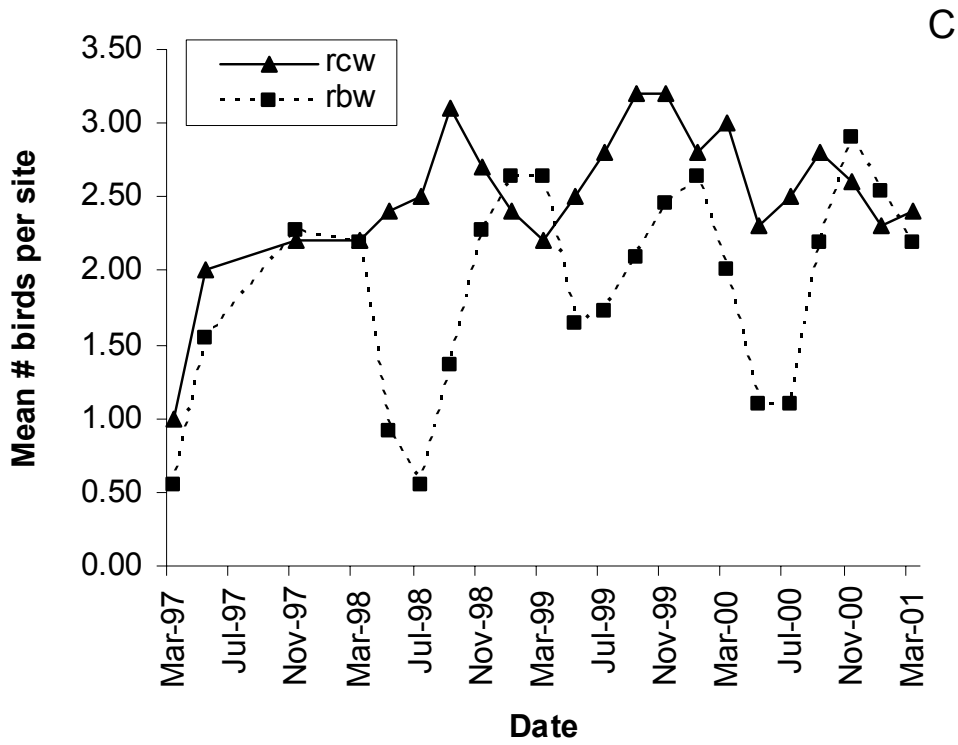


Figure 7C. The mean number of red-cockaded woodpeckers and red-bellied woodpeckers in control sites. N = 10 (control), N = 11 (removal) in the WRD. Data shown spans 4 years (March 1997 to March 2001)

Table 14. Variation in estimates of competitive interactions between red-cockaded woodpeckers (RCW) and red-bellied woodpeckers (RBW) at the individual and the population level.

	Individual (observational)	Individual (experimental)	Population (experimental)
Direction of Competition	Asymmetrical RBW → RCW	Symmetrical RCW ↔ RBW	Asymmetrical / Symmetrical RCW ↔ RBW RBW → RCW
Nature of Interactions	Contramensal RBWs + RCWs –	Tree holes equally likely to be occupied by RCWs or RBWs	RCW group size ↓ ♀ retention ↓ RCW productivity unaffected
Source	Kappes (1997)	Walters and James (unpub ms)	This study.

able to obtain tree holes without having to expend the energy associated with excavation. In my experimental studies (Walters and James unpub ms) individual red-bellied and red-cockaded woodpeckers interacted reciprocally through both interference and exploitative competition over time scales of a few days. Once the tree holes are in place, these two species may be relatively equal competitors, rather than as a kleptoparasite and a host.

The goal of the experiment reported here was to look for negative population-level effects of red-bellied woodpeckers on red-cockaded woodpeckers. I was not able to remove red-bellied woodpeckers, so the original hypothesis could not be tested. At the population level in 1999 I found that, in sites where I removed red-bellied woodpeckers, red-cockaded woodpecker nests were proportionally less successful than nests in control sites (Table 11). The red-cockaded woodpecker group size in removal sites remained lower than that in the controls sites. In 1999 the numbers of red-cockaded woodpeckers in the control clusters were higher than normal levels. I am unsure of the mechanism but results suggest that the disruptive nature of immigrating red-bellied woodpeckers affected red-cockaded woodpeckers negatively. These new red-bellied woodpecker individuals may disrupt the assemblage. In the declining WRD population, only 44% of females remained from one year to the next. That value was reduced to only 20% where red-bellied woodpeckers were removed. It appears that immigrating red-bellied woodpeckers are having a severe effect on the persistence of female red-cockaded woodpeckers.

I was attempting to completely remove red-bellied woodpeckers from the assemblage but it was impossible. Floater red-bellied woodpeckers (*sensu* Zack and Stutchbury 1992) within the population were constantly immigrating into my experimental sites and disrupting the equilibrium. In contrast, control sites had red-bellied woodpeckers present but their presence was relatively stable with respect to their fidelity to individual tree holes, much in the way of familiar neighbors (i.e. “dear enemies”, Temeles 1994). In 1999, there was an exceptionally high number of red-bellied woodpeckers. In

“typical” years the population of red-bellied woodpeckers in control clusters reaches its lowest level in July but in 1999 populations were at least 50% higher.

There were over twice as many red-bellied woodpeckers removed from the WRD than from the ARD per unit effort and the number of trees with available tree holes per cluster is 36% higher in the WRD than the ARD (Table 9). Partly because of the rate of prescribed burning in the WRD, it tends to have more trees with old tree holes. Given a sufficient number of tree holes within a red-cockaded woodpecker cluster, more than one pair of red-bellied woodpeckers can be present.

By making weekly visits to weekly removal sites in the ARD, I was able to increase the number of birds removed by 37%. But, even by making the extra visits in weekly treatments, this percentage was still lower than that of my bimonthly visits in the WRD. Apparently, there is a remarkably high population of red-bellied woodpeckers available to immigrate to available sites in the WRD, especially from November to March, when young of the year were dispersing. Lowest occupancy rates for red-bellied woodpeckers occurred in July, late in the breeding season. This period also coincides with the occupancy of available tree holes by migrants and their offspring (e.g. eastern bluebirds, great crested flycatchers).

The longer-term data in the WRD allowed us to track the relative abundances of red-bellied woodpeckers and red-cockaded woodpeckers over 4 years in control clusters. Without competitive interactions, I would expect the populations to track one another. However, I found that rises in red-bellied woodpecker abundance were followed by decreases in red-cockaded woodpecker numbers. The implication is that the species are competing for tree holes and that the number of suitable tree holes is limiting.

In order to understand the full extent of the nature of competitive interactions, one should be cognizant of the differences between experimental approaches that examine the level of the individual as in contrast to those that look at the level of the population. Most of my findings point towards reciprocal interactions at the individual level between the two species (Walters and James unpub ms). However, the experiments reported

here offer strong support for asymmetric competitive effects on adult female red-cockaded woodpeckers due to the influx of red-bellied woodpeckers. This population-level effect, which I exaggerated through experimental manipulation, is probably contributing to the population of red-cockaded woodpeckers in the WRD. Studies like mine should remind researchers that observations of behavioral interactions, while important, should not be generalized to the population level until experiments can clarify their fitness consequences at the population level

3. ESTIMATING COMPETITIVE INTERACTIONS USING MARKOV CHAIN MODELS: A TERRESTRIAL EXAMPLE

Introduction

Markov transition probability matrices have been used to model community succession in many systems (e.g. forests, Waggoner and Stephens 1970, Horn 1975, Enright and Ogden 1979, Usher 1979, Rego et al. 1993, Korotkov 2001; alpine areas, Lough et al. 1987; plant communities, McAuliffe 1988, Yeaton and Bond 1991, Childress et al. 1998; coral reefs, Tanner et al. 1994, Wootton 2001a; and rocky intertidal, Wootton 2001b, Hill et al. 2002). One criticism of such applications has been that they lack rigorous tests of Markovian assumptions (Facelli and Pickett 1990). In particular, Facelli and Pickett assert that empiricists have not examined temporal or spatial effects on Markovian properties. Recently, Caswell (2001) and Hill et al. (2002) have proposed a method that can be used for such tests. The goal of this study is to apply Markov-process analyses to examine the species interactions in an assemblage that uses a dynamic, yet discrete resource. The system I describe is unusual in the sense that only one individual at a time occupies a “patch” of resource. The turnover of individuals in the species assemblage is examined and the effects of competitive interactions on the species assemblage are determined by manipulating potential competitors.

First I describe the assemblage of species using tree holes for roosting and nesting in longleaf pine (*Pinus palustris*) forests. The red-cockaded woodpecker (*Picoides borealis*), an endangered species in the longleaf pine ecosystem, create holes in living

pinus (USFWS 2003). These holes can take from 6 to 15 years to complete (Conner and Rudolph 1995a, Harding 1997). Tree holes are typically excavated in mature trees that are usually greater than 100 years old (Hovis and Labisky 1985, Rudolph and Conner 1991, James et al. 1997) and are infected with red heart fungus (Jackson 1977). Once created, the tree holes can be used for as long as 30 years by successive generations of red-cockaded woodpeckers (Conner and Rudolph 1995a). However, as tree holes age, red-cockaded woodpeckers are increasingly likely to abandon them and create newer holes in other trees. Over time, the tree holes accumulate in the defended area of a family group of woodpeckers and the area of trees with holes is referred to as the “cluster” (Walters et al. 1988).

Red-cockaded woodpeckers are cooperative breeders that retain their family group throughout the year (Ligon 1970). They may have evolved the ability to create tree holes in living pines because the live trees, being relatively tolerant of frequent fires in their fire prone environment, provide safe nest and roost sites (Conner et al. 2001). Reasons for abandoning a particular tree hole for roosting can include dispersal, usurpation by another individual, damage to the hole or tree from fire or decay (Conner and Locke 1979), inundation of the hole with rainwater (Walters and Kneitel 2004), death of the tree from insect infestation (Conner and Rudolph 1995b), damage to the tree at the hole from wind (Conner et al. 1991, Conner and Rudolph 1995c), or death or deterioration of the tree from natural causes (Ligon 1970).

Various species of birds, mammals, amphibians, reptiles, and invertebrates also use tree holes originally excavated by red-cockaded woodpeckers for roosting or nesting. Because no other species besides the red-cockaded woodpecker excavates tree holes in living pine trees, it is integral to the assemblage, in the sense of serving as a keystone species (USFWS 2003). Other excavating species can enlarge existing tree holes in both living and dead trees and, through time, the dimensions of the tree hole increase. Because of these modifications by other species (i.e. consumer-dependent processing) and through decay and weathering (i.e. consumer-independent processing), the system can be viewed as an example of a processing chain (*sensu* Heard 1994). The entrance diameter of a tree hole made by a red-cockaded

woodpecker appears to be one of the best predictors of the species that will use it (Conner et al. 1976, pers. obs). Thus, species that enlarge smaller tree holes are providing a new resource to those that use larger tree holes. The species that used tree holes in my study have been found (here and elsewhere) to prefer tree holes, in order of increasing hole size as follows: red-cockaded woodpecker, red-bellied woodpecker (*Melanerpes carolinus*), southern flying squirrel (*Glaucomys volans*), eastern bluebird (*Sialia sialis*), great crested flycatcher (*Myiarchus crinitus*), eastern screech owl (*Otus asio*), and pileated woodpecker (*Dryocopus pileatus*, pers. obs., Rudolph et al. 1990). Other less common species found using red-cockaded woodpecker tree holes include, but are not limited to, red-headed woodpecker (*Melanerpes erythrocephalus*), northern flicker (*Colaptes auratus*), brown-headed nuthatch (*Sitta pusilla*), squirrel tree frog (*Hyla squirella*), gray rat snake (*Elaphe obsoleta spiloides*), corn snake (*Elaphe guttata*), broad-headed skink (*Eumeces laticeps*), and various Hymenoptera (pers. obs., Rudolph et al. 1990, Conner et al. 1997). By considering only those species that use tree holes originally excavated by red-cockaded woodpeckers, the assemblage can be clearly defined. Having a discrete resource such as a tree hole makes experimental manipulation tractable and makes the system conducive to investigations of the succession of species within the hole-using assemblage.

Previous research examining the nature of interactions between red-cockaded woodpeckers and red-bellied woodpeckers, the two most numerically dominant species in the assemblage, varied with the experimental approach. In a study that examined short-term behavioral interactions among individuals, competition was symmetrical in that each species competed equally for tree holes (Walters and James, unpub ms). In a separate study examining the population-level effect of one species on the other, some types of competitive interactions were asymmetric and some were symmetric (Walters and James unpub ms). This third study, conducted at the community level will allow a third comparative approach. It will examine the nature of the interactions of the two focal species, while controlling for the effect of the rest of the assemblage. This study is the first to explore a Markovian process in a system in which (a) only one organism

occupies each “patch” and (b) the assumptions of 1st order Markovian transitions are tested for temporal and spatial variation.

Markov Chain Models

Following the terminology used by Hill et al. (2002), I describe a Markov chain model for community succession in occupants of red-cockaded woodpecker tree holes. Each hole is viewed as a point in space (l) that can be occupied at time (t) by an individual organism. The community at any given t is determined by the probability vector $x(t)$, whose i th element x_i is the probability that a tree hole is occupied by species i at time t :

$$x(t+1) = A^{(t,l)}x(t); \quad (1)$$

where $0 \leq x_i \leq 1$, $\sum_i x_i = 1$ and $A^{(t,l)}$ is a column-stochastic transition matrix describing successional dynamics for $t, t+1$ at space l . Thus, matrix entry $a_{ij}^{(t,l)}$ gives the probability that a tree hole is occupied by species i at time $t + 1$, given that it was occupied by species j at time t . If the transition matrix is homogeneous, so that $A^{(t,l)} = A$, and if A is primitive, then $x(t)$ converges from any initial condition to an assemblage proportional to the right eigenvector \mathbf{u} corresponding to the dominant eigenvalue λ of A . Thus, \mathbf{u} is a prediction of the species assemblage in a constant environment (Hill et al. 2002).

Methods

Field methods

This study was conducted in the Apalachicola National Forest in northern Florida (USA). This 228 865 ha forest is divided into an eastern Wakulla Ranger District (WRD, 111 866 ha) and a western Apalachicola Ranger District (ARD, 116 999 ha) management unit. It supports 17% of all remaining red-cockaded woodpeckers (USFWS 2003). However, the WRD supports at most 138 family groups and that population is estimated to have declined by 20% in the past 5 years (pers. obs.), whereas the ARD is estimated to support 486 family groups and that population appears to be stable (USFWS 2003). The woodpeckers occur mostly in stands of

naturally regenerated open pine woods that are managed by frequent prescribed burning and thinning (James et al. 1997, James et al. 2001). In the WRD, 11 management compartments ($\bar{X} = 1\,099$ ha) were randomly selected from among 96 compartments that contained at least two red-cockaded family groups. Within each of the 11 compartments, I randomly assigned one of the clusters to a control group and one to a red-bellied woodpecker bimonthly removal group. The WRD experiment was carried out from March 1997 until March 2001 but I only report data from May 1999 until March 2001 in order to use the same temporal reference when comparing management districts. In the ARD, 14 management compartments ($\bar{X} = 1\,292$ ha) were randomly selected from among 57 compartments, each of which contained at least four red-cockaded family groups. Within each of the 14 compartments, I randomly assigned one of the clusters to a control group, one to a red-bellied woodpecker bimonthly removal group (i.e. a sequential pulse experiment, *sensu* Bender et al. 1984), and one to red-bellied woodpecker weekly removal group (i.e. a sustained press experiment). The ARD experiment was carried out from June 1999 until April 2001. Most of the control groups were part of a larger-scale experiment in fire ecology.

Red-bellied woodpeckers were permanently removed from bimonthly removal clusters by visiting the clusters at night and removing birds from tree holes in which they were roosting. The removed individuals were initially relocated but even those that were moved more than 30 km returned to their capture site within a few days. Red-bellied woodpeckers were removed from weekly removal clusters by visiting the sites during the day, playing a tape of red-bellied woodpecker vocalizations, and shooting them. All clusters were visited bimonthly and all red-bellied woodpeckers were removed from experimental clusters during those visits. The red-bellied woodpeckers that were removed are now housed in the collection at the University of Florida Museum of Natural History.

All red-cockaded woodpecker groups in this study had been monitored for several years before the study and the number and location of all tree holes was known (WRD $\bar{X} = 9.95$ tree holes per cluster, range = 6—17, N = 22 clusters; ARD: $\bar{X} = 6.55$ tree

holes per cluster, range = 3—10, N = 42 clusters). During the experimental monitoring, the species identity of every tree-hole occupant was noted.

Transition data were obtained by visiting tree holes bimonthly at night and surveying tree-hole occupants from the ground by shining a flashlight towards the hole entrance and observing any occupants that peered outwards. If no occupants were apparent using the first method, an infrared camera mounted on the end of a 15-m telescoping fiberglass pole (Furhman Diversified, Inc.; Seabrook, Texas, USA) was inserted into the tree hole. Thus, each transition represents a change in the species state of a given tree hole within a cluster. I recorded the species occupying each tree hole in each cluster bimonthly for a total of 5,526 tree-hole observations.

Parameter estimation

To estimate transition matrices, I constructed a five-way contingency table N of size 7 x 7 x 11 x 11 x 2 in the WRD and of size 7 x 7 x 11 x 14 x 3 in the ARD. Tree-hole occupants were classified by their state (*S*) at time *t*, their fate (*F*) at time *t*+1, the time (*T*) of the observation, location (*L*), treatment (*R*), and management district (*D*) of the cluster. The entry n_{ijtlrd} in cell (*ijtlrd*) of the table gives the number of tree-hole occupants making the transition from state *j* (7) to fate *i* (7) at time *t* (11) in location *l* (11 or 14) in treatment *r* (2 or 3) in district *d* (2) (terminology after Caswell 2001, Hill et al. 2002). Due to sample size constraints, the eleven 2-month time intervals were collapsed into three time categories (6 months per category) and the locations (i.e. cluster sites) in the WRD were grouped into five pairs based upon geographic proximity to one another, where needed.

From table N, I constructed 5 sets of transition matrices:

1. A set of 6 (*t* x *r*) time-treatment specific matrices, $A^{(tr)}$, $t = 1, \dots, 3$ (collapsed 11 time intervals into 3 6-month intervals); $r = 1, 2$, in which the effects of location are ignored in the WRD. The maximum likelihood estimates $\hat{a}_{ij}^{(tr)}$ of the entries of $A^{(tr)}$ are

$$\widehat{a}_{ij}^{(tr)} = \frac{\sum_{l=1}^{11} n_{ijlr}}{\sum_{l=1}^{11} \sum_{i=1}^7 n_{ijlr}} \quad (2)$$

That is, $\widehat{a}_{ij}^{(tr)}$ is the number of observations moving from state j to state i at time t in treatment r , divided by the total number of observations starting in state j at time t and treatment r , all 11 sites combined.

2. A set of 10 location-treatment specific matrices, $A^{(lr)}$, $l = 1, \dots, 5$ (collapsed 11 compartments into 5 2-compartment pairings); $r = 1, 2$, in which the effects of time are ignored (i.e. all times combined) in the WRD. The maximum likelihood estimates $\widehat{a}_{ij}^{(lr)}$ of the entries of $A^{(lr)}$ are

$$\widehat{a}_{ij}^{(lr)} = \frac{\sum_{l=1}^{11} n_{ijlr}}{\sum_{l=1}^{11} \sum_{i=1}^7 n_{ijlr}} \quad (3)$$

3. . A set of 6 time-treatment specific matrices, $A^{(tr)}$, $t = 1, \dots, 3$ (collapsed 11 time intervals into 3 6-month intervals); $r = 1, 2$ (excluding press treatment) in which the effects of location are ignored in the ARD. The maximum likelihood estimates $\widehat{a}_{ij}^{(tr)}$ of the entries of $A^{(tr)}$ are

$$\widehat{a}_{ij}^{(tr)} = \frac{\sum_{l=1}^{14} n_{ijlr}}{\sum_{l=1}^{14} \sum_{i=1}^7 n_{ijlr}} \quad (4)$$

4. A set of 9 time-treatment specific matrices, $A^{(tr)}$, $t = 1, \dots, 3$; $r = 1, \dots, 3$ (including press treatment) in which the effects of location are ignored in the ARD. The maximum likelihood estimates $\widehat{a}_{ij}^{(tr)}$ of the entries of $A^{(tr)}$ are

$$\widehat{a}_{ij}^{(tr)} = \frac{\sum_{l=1}^{14} n_{ijlr}}{\sum_{l=1}^{14} \sum_{i=1}^7 n_{ijlr}} \quad (5)$$

5. A set of 4 treatment-district specific matrices, $A^{(rd)}$, $r = 1,2$ (excluding press treatment); $d = 1,2$ in which the effects of location and time are ignored in the entire forest. The maximum likelihood estimates $\hat{a}_{ij}^{(rd)}$ of the entries of $A^{(rd)}$ are

$$\hat{a}_{ij}^{(rd)} = \frac{\sum_{t=1}^{11} \sum_{l=1}^{11} n_{ijrd}}{\sum_{t=1}^{11} \sum_{l=1}^{11} \sum_{i=1}^7 n_{ijrd}} \quad (6)$$

I use loglinear analysis to examine differences among matrices. The logarithm of the number of transitions is modeled as a linear function of the effects of each variable under consideration and their respective interactions. The models are defined by using the highest order interactions (Caswell 2001, Hill et al. 2002). The models are hierarchical so any interaction terms included also involve lower order interactions.

This study includes Fate as the response variable and includes explanatory variables State, Time, Location, Treatment, and District. All of the models I describe use Fate and the interaction of all other terms under consideration for that particular model (Fingleton 1984, Caswell 2001). The null hypothesis in tests for differences among Markov chains is one of conditional independence such that Fate at time $t + 1$ is conditional on State at time t but independent of any other variables including time, location, or treatment.

I fit all of the loglinear models using Statistica (Statsoft, Inc. 2000). In order to choose the best model that best approximated the factors contributing to the transition data, I used Akaike Information Criteria (AIC). AIC is an estimate of the expected, relative distance between the fitted model and the unknown true mechanism that generated the observed data (Burnham and Anderson 2002). For loglinear models of the type I describe,

$$AIC = G^2 - 2(df), \quad (7)$$

where G^2 is the goodness-of-fit likelihood statistic and df is the degrees of freedom of the model (Caswell 2001). One looks for the smallest AIC as the best compromise

between goodness-of-fit and parsimony (Hill et al. 2002). The difference in AIC values between competing models, after being scaled to the best model (i.e. that with the lowest AIC), can provide estimates of the level of empirical support for the alternative model relative to the best model. Generally, ΔAIC of 0-2 provides substantial support for the alternative model, ΔAIC of 4-7 provides considerably less support, and ΔAIC of > 10 provides no support (Burnham and Anderson 2002).

I used the transition probabilities to project the matrices in order to determine the equilibrium distribution of species. I calculated the rate of convergence to equilibrium by using the damping ratio: $\rho = \lambda_1/|\lambda_2|$, where λ_1 and λ_2 are the first and second largest eigenvalues of the matrix under consideration. The assemblage will transition towards equilibrium in an exponential manner. The half-life from perturbation of an assemblage to equilibrium is $\log 2 / \log \rho$ (Caswell 2001).

I calculated the community index of complexity, a term analogous to connectance in food web analyses (May 1972), by taking the observed number of transitions in the matrix as a proportion of all possible transitions (Tanner et al. 1994).

Results

A total of 21 species groups were found occupying tree holes in the study system, consisting of seven state categories (Table 15). The matrix was collapsed to ensure adequate sample sizes in each category (Moloney 1988, Caswell 2001). The seven state variables correspond to two single species (red-cockaded woodpeckers, red-bellied woodpeckers), one functional group consisting of squirrels (southern flying squirrels, gray squirrels [*Sciurus carolinensis*], fox squirrel [*Sciurus niger*]), empty tree holes, water-filled tree holes (temporarily unusable), a functional group consisting of non-nesting tree-hole users including herpetofauna (corn snakes, gray rat snakes, squirrel tree frogs, broad-headed skinks) and invertebrates (wasps, scorpions, ants, beetles, mud daubers), and a functional group consisting of other avian species that use tree holes for reproduction (great crested flycatchers, eastern bluebirds, pileated

Table 15. Species occupying red-cockaded woodpecker tree holes during bimonthly surveys (May 1999–April 2001) in the Apalachicola National Forest (N = 25 control clusters, N = 39 removal clusters), northern Florida, collapsed into 7 model states (State ID). The number of observations counted per state is shown in the right-hand column (N = 5526 total observations). The state SFS (x_3) corresponds to a functional group of squirrels (mostly southern flying squirrels), EMP (x_4) is an empty tree hole, WAT (x_5) is a tree hole that is filled with water, HIN (x_6) is a group of 8 ecologically minor herpetofauna and invertebrates, and BIR (x_7) is a group of 7 ecologically minor avian species.

Xi	Model States	Species type(s)	State ID	Number of Observations
1	Red-cockaded woodpecker	Bird	RCW	1870
2	Red-bellied woodpecker	Bird	RBW	816
3	Southern flying squirrel Gray squirrel Fox squirrel	Squirrels	SFS	573
4	Empty		EMP	1754
5	Water		WAT	205
6	Gray Rat snake Corn snake Broad-headed skink Squirrel tree frog Wasps Scorpion Ants Beetles Mud daubers	Herpetofauna & Invertebrates	HIN	125
7	Great crested flycatcher Eastern bluebird Pileated woodpecker Northern flicker Red-headed woodpecker Eastern screech owl Brown-headed nuthatch	Minor Birds	BIR	183
	Total			5 526
				(N = 619 tree holes)

woodpeckers, northern flickers, red-headed woodpeckers, eastern screech owls, and brown-headed nuthatches).

Red-bellied Woodpecker Removal Study

Wakulla Ranger District

Within the WRD, when comparing the effect of Time and Treatment, the null model was most strongly supported (AIC = -215.5) and no alternative models were supported. I found no effect of Time ($\Delta G^2 = 93.4$, $\Delta df = 84$, $p = 0.226$) on the transitions when I pooled transition data over all locations (Figure 8). There was a significant effect of red-bellied woodpecker bimonthly removal ($\Delta G^2 = 66.9$, $\Delta df = 42$, $p = 0.009$) on the transitions but there was no evidence of interaction between Time and Treatment ($\Delta G^2 = 45.6$, $\Delta df = 84$, $p = 0.999$).

Within the WRD, when comparing the effect of Location and Treatment, the null model was most strongly supported (AIC = -401.0) and no alternative models were supported. I found no effect of Location ($\Delta G^2 = 157.1$, $\Delta df = 168$, $p = 0.716$) on the transitions when I pooled transition data over all time intervals (Figure 9). As before, there was a significant effect of red-bellied woodpecker bimonthly removal ($\Delta G^2 = 73.5$, $\Delta df = 42$, $p = 0.001$) on the transitions and there was no evidence of interaction between Location and Treatment ($\Delta G^2 = 122.3$, $\Delta df = 168$, $p = 0.997$).

The equilibrium condition for WRD control sites revealed that the occupancy of red-cockaded woodpeckers and red-bellied woodpeckers are projected to be similar, 26% and 24%, respectively (Figure 10). Southern flying squirrels are projected only at 7%, with almost one third of available tree holes remaining empty. In the bimonthly red-bellied woodpecker removal sites, the projection is that red-cockaded woodpeckers will be slightly less abundant than they were in the control sites. Red-bellied woodpeckers, because they were being removed, are projected to have an abundance close to 14%, but not the 0% one might expect if all individuals had been constantly removed. Flying squirrels, however, are predicted to increase 2.4 times over what they were in the

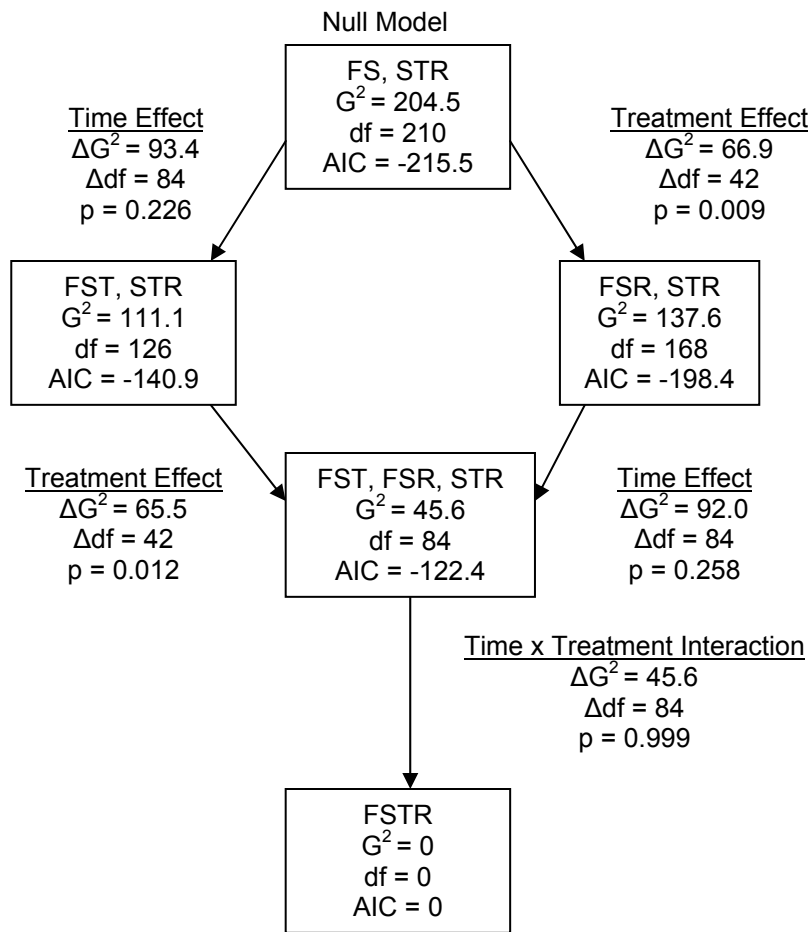


Figure 8. Loglinear analysis for the effects of Time (3 x 6-month intervals) and Removal Treatment (control, bimonthly) on tree-hole transition data (all sites pooled within treatment, N = 11) in the Wakulla Ranger District. Each box represents a particular model and shows the goodness of fit G^2 statistic, degrees of freedom, and the Akaike Information Criteria value. The uppermost box is the null model (Fate depends on State). Lower boxes represent models that include higher-order interactions between Fate and Time, Treatment, or both. Terms added to each model, along with the corresponding changes in G^2 (ΔG^2), degrees of freedom (Δdf), and corresponding probability value are shown along the arrows (after the format of Caswell 2001, Hill et al. 2002).

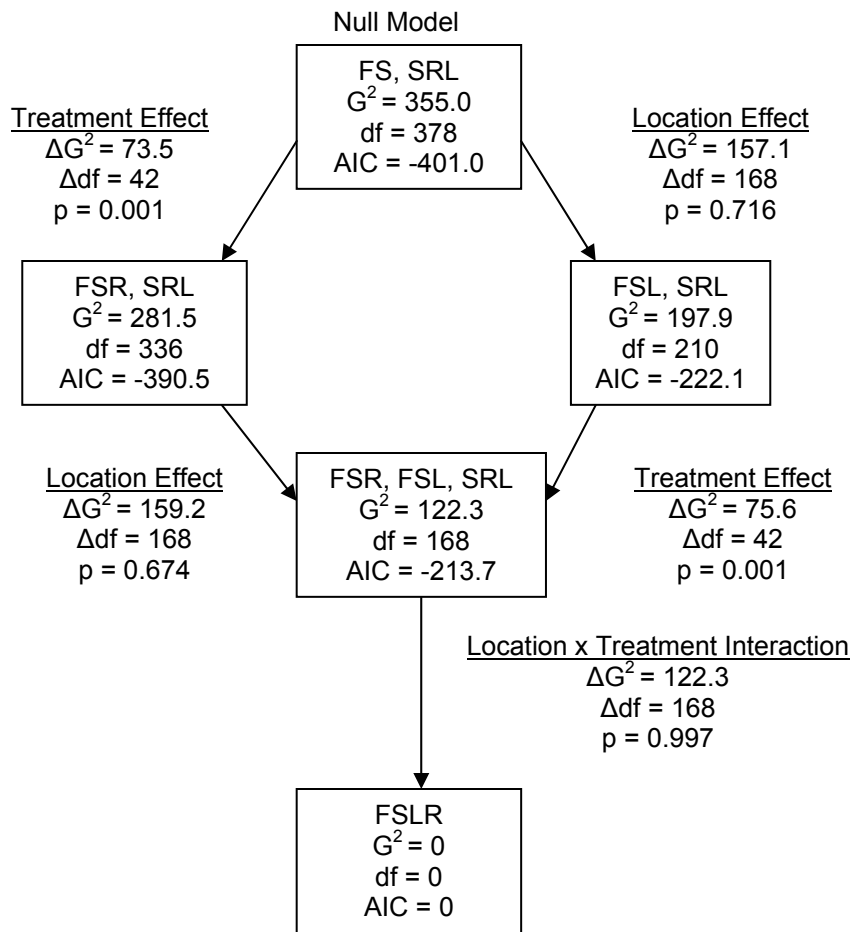


Figure 9. Loglinear analysis for the effects of Location (5 x 2-sites combined) and Removal Treatment (control, bimonthly removal) on tree-hole transition data (all sites pooled within treatment, N = 11) on the Wakulla Ranger District.

A

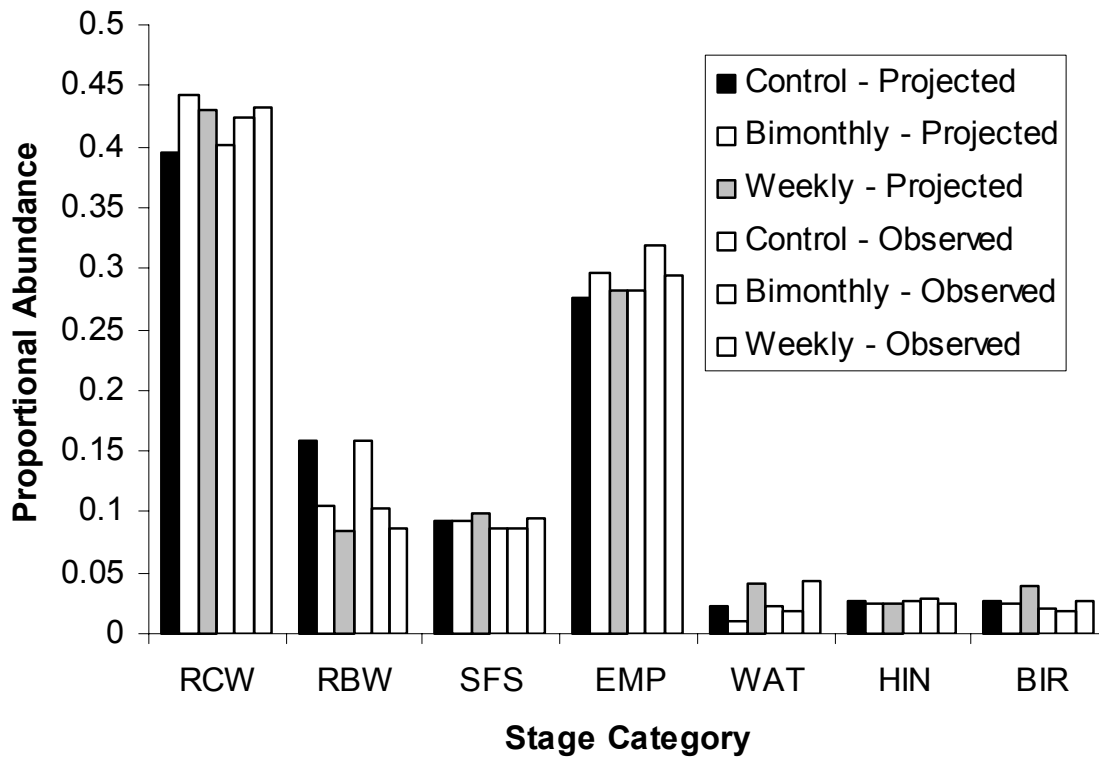


Figure 10A. Projected equilibrium condition and observed proportional abundance for state variable in each of the treatments in the Apalachicola Ranger District. See Table 1 for species codes.

B

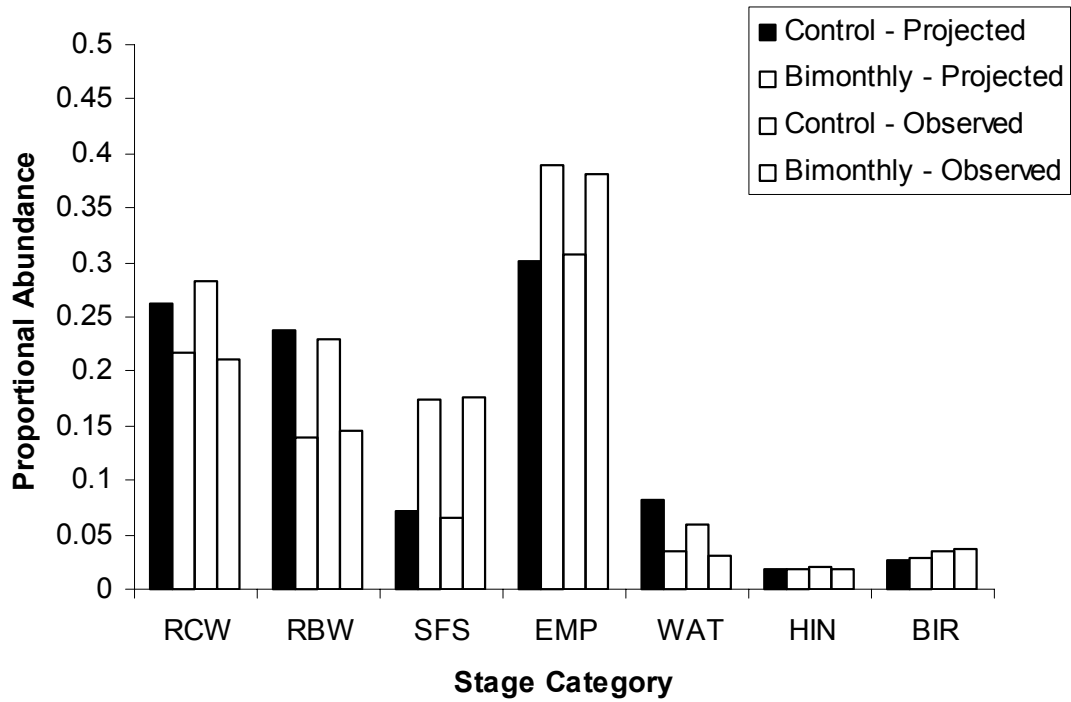


Figure 10B. Projected equilibrium condition and observed proportional abundance for state variable in each of the treatments in the Wakulla Ranger District. See Table 1 for species codes.

control sites and to exceed the proportional abundance of red-bellied woodpeckers. These projected proportional abundances closely approximate observed relative abundances, indicating the assemblage is close to equilibrium condition.

Apalachicola Ranger District

In the ARD, when comparing the effect of Time and Treatment (only control and bimonthly removal), the null model was most strongly supported (AIC = -263.9) and no alternative models were supported (Figure 11). I found no effect of Time ($\Delta G^2 = 84.5$, $\Delta df = 84$, $p = 0.464$) or Treatment ($\Delta G^2 = 33.1$, $\Delta df = 42$, $p = 0.853$) on the transitions when I pooled transition data over all locations, nor was there evidence of interaction between Time and Treatment ($\Delta G^2 = 38.5$, $\Delta df = 84$, $p = 0.999$) in the model.

Within the ARD, when comparing the effect of Time and Treatment (control, bimonthly, weekly removal), the null model was most strongly supported (AIC = -413.3) and no alternative models were supported (Figure 12). I found no effect of Treatment when I added the weekly removal treatment to the analysis ($\Delta G^2 = 63.8$, $\Delta df = 84$, $p = 0.951$) when I pooled over all locations. There was, however, a significant effect of Time ($\Delta G^2 = 122.6$, $\Delta df = 84$, $p = 0.004$) for the model that included the weekly removal treatments. Again, there was no interaction between Time and Treatment ($\Delta G^2 = 73.4$, $\Delta df = 168$, $p = 1.000$).

Red-cockaded woodpeckers are projected to be the most abundant tree-hole occupant when equilibrium conditions are met (Figure 10). They are 2.5 times more abundant than red-bellied woodpeckers. Southern flying squirrels are projected to be a little lower in abundance than red-bellied woodpeckers. Removal of red-bellied woodpeckers bimonthly and weekly causes red-cockaded woodpecker numbers to increase slightly over control projections. The removals serve to decrease the predicted numbers of red-bellied woodpeckers, but only marginally. Flying squirrels seem unaffected by red-bellied woodpecker removals. Projected values are similar to observed relative abundances, indicating the assemblage is close to equilibrium.

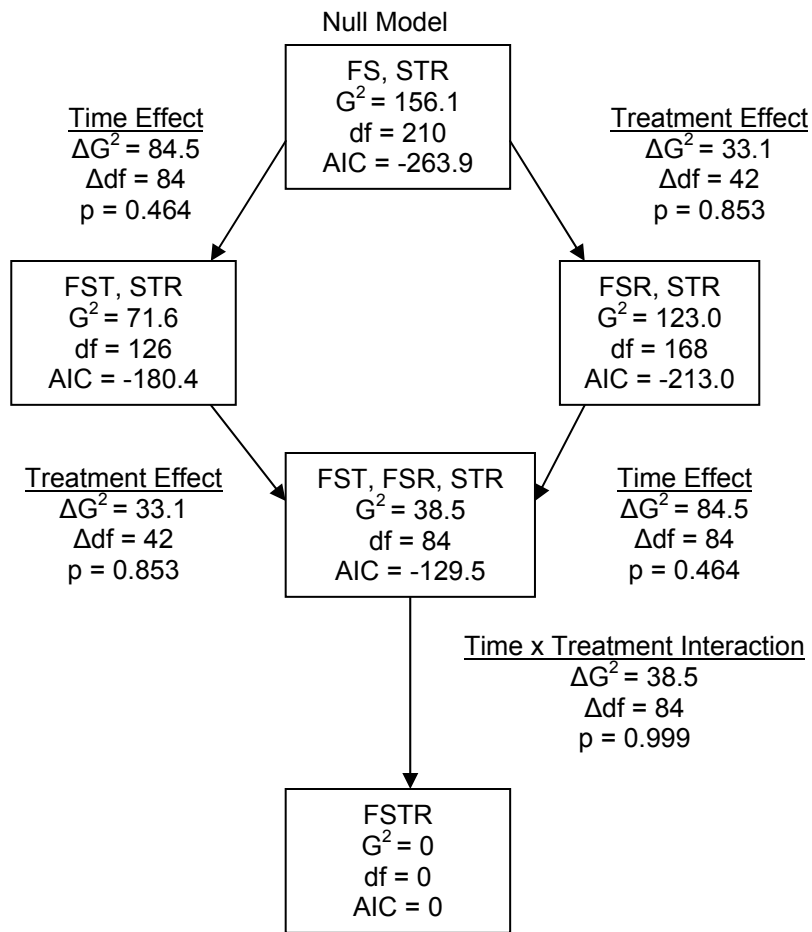


Figure 11. Loglinear analysis for the effects of Time (3 x 6-month intervals) and Removal Treatment (control, bimonthly) on tree-hole transition data (all sites pooled within treatment, N = 14) on the Apalachicola Ranger District.

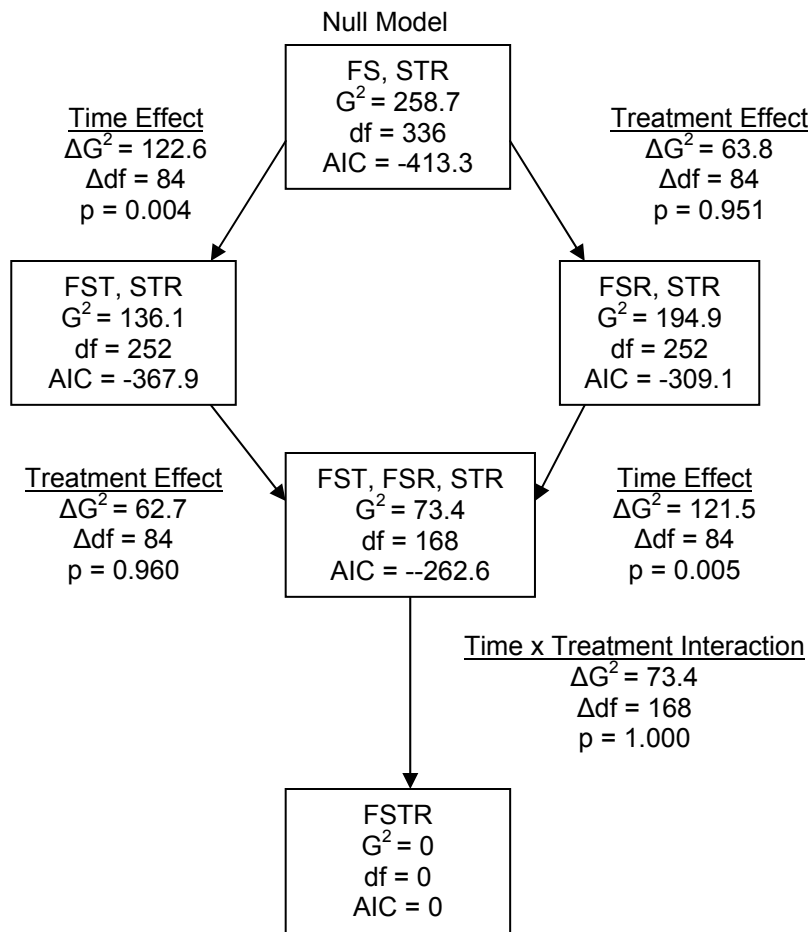


Figure 12. Loglinear analysis for the effects of Time (3 x 6-month intervals) and Removal Treatment (control, bimonthly, weekly removal) on tree-hole transition data (all sites pooled within treatment, N = 14) on the Apalachicola Ranger District.

Apalachicola Ranger District vs Wakulla Ranger District

When comparing management districts and treatments (control, bimonthly), the null model was most strongly supported (AIC = -80.1) and no alternative models were supported (Figure 13). I found a significant effect of Treatment ($\Delta G^2 = 70.1$, $\Delta df = 42$, $p = 0.004$) and District ($\Delta G^2 = 69.1$, $\Delta df = 42$, $p = 0.005$), when I pooled over all times and locations within a district. There was no interaction between Treatment and District ($\Delta G^2 = 32.8$, $\Delta df = 42$, $p = 0.844$).

Red-cockaded woodpeckers are projected to be 1.5 times more abundant in the ARD than in the WRD (Figure 10). Conversely, red-bellied woodpeckers are projected to be 1.5 times more abundant in the WRD. Southern flying squirrels are of about equal abundance on either management district. Despite the fact that there are more tree holes per red-cockaded woodpecker cluster in the WRD, the proportion projected to remain empty is about the same on both districts (ARD: 27%, WRD: 30%). The most striking difference between the two districts is the compensatory relationship between red-bellied woodpeckers and southern flying squirrels in the WRD removal sites. This relationship is not predicted for the ARD.

The assemblage is predicted to reach equilibrium, following disturbance, with a half-life (damping ratio) of approximately 5 months (Table 16). The community can recover slightly faster on the WRD than the ARD. In addition, the matrices developed for the WRD had higher community indices of complexity (0.897–0.918) than the ARD (0.755–0.857, Table 16). Relative to control sites, removal treatments in both populations resulted in a higher community complexity index.

Discussion

The removal of red-bellied woodpeckers in the WRD caused changes in the species transitions. The finding of no effects of time supports the time-invariant assumptions of Markov processes. The finding that location within a management district had no effect on community interactions is noteworthy. It supports the contention that the dynamics

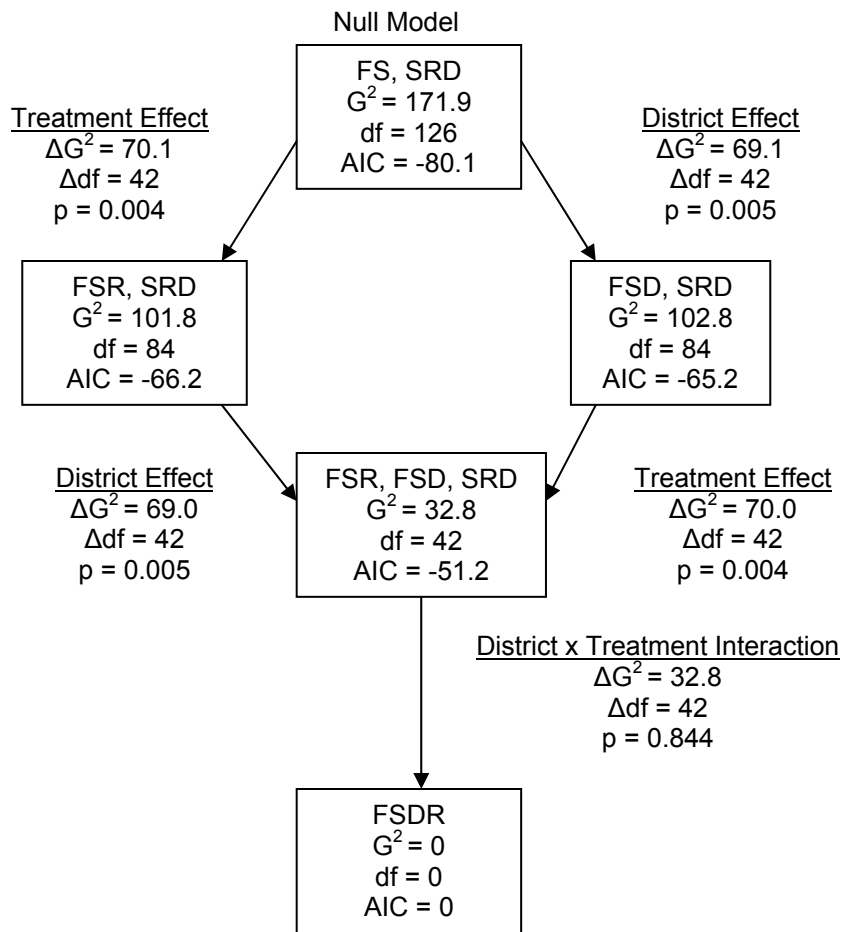


Figure 13. Loglinear analysis for the effects of Treatment (control, bimonthly) and management district on tree-hole transition data (all sites pooled within treatment, N = 14 ARD, N=11 WRD). The ARD data were corrected to account for the differences in sample sizes between districts.

Table 16. Damping ratios ($\rho = \lambda_1/|\lambda_2|$) and community index of complexity metrics for the treatments in the Apalachicola Ranger District and the Wakulla Ranger District.

District	Treatment	Damping Ratio $\rho = \lambda_1/ \lambda_2 $	Half-life (months)	Community Complexity
ARD	Control	1.318	5.02	0.755
	Bimonthly	1.313	5.09	0.837
	Weekly	1.295	5.36	0.857
WRD	Control	1.333	4.82	0.939
	Bimonthly	1.339	4.75	0.918

among species are similar over the entire management district and, thus, it is safe to pool sites.

By comparison, when considering only the bimonthly red-bellied woodpecker removal treatment in the ARD, there was no effect of removal treatment. The same effort was used in the removal of red-bellied woodpeckers in bimonthly treatments on both management districts. Red-bellied woodpeckers apparently play a much larger role in the species dynamics in the WRD than in the ARD. Removal of red-bellied woodpeckers in the ARD did not affect species interactions. From previous work (Walters and James unpub ms), it was shown that the rate of red-bellied woodpecker immigration is greater in the WRD following removal of individuals. This constant pressure of immigration of red-bellied woodpeckers into red-cockaded woodpecker clusters causes more interaction among members of the assemblage in the WRD. What this Markov process study reveals is that there appears to be an interaction between red-bellied woodpeckers and southern flying squirrels in the WRD, a relationship that had been undetected until now. Following removal of red-bellied woodpeckers in the WRD, the projected proportional abundance of southern flying squirrels increased. The predicted reduction in red-cockaded woodpecker abundance may be caused by the increase of southern flying squirrels, mediated through the removal of red-bellied woodpeckers. There was no evidence of this interaction among the three species in the ARD.

Interestingly, when the weekly removal treatment was included in the matrix analysis in the ARD, I found that the model still did not support a treatment effect. There was, however, an effect of time when this treatment was added to the analysis. The interpretation is that the effect of the weekly removal of red-bellied woodpeckers changed over time. This finding could be caused by the fact that eventually enough immigrating red-bellied woodpeckers were removed to lower the supply of immigrating floaters (see also Walters and James unpub ms). However, the overall effect of red-bellied woodpeckers in this management district was low enough that the change over time in weekly removal clusters did not manifest itself in a treatment-level effect.

The comparison of districts using only the control and bimonthly sites showed a strong effect of treatment and district. Given the previous findings for each district taken individually, my interpretation is that the red-bellied woodpeckers in the WRD exert a greater overall effect on the species assemblage than do red-bellied woodpeckers in the ARD, most likely due to their greater relative abundance in the WRD.

Overall, all the experimental models supported the null model, meaning that the best predictor of occupancy was the species identity of the occupant in the previous time step. These experiments show the utility and importance of testing Markov transition matrices for the effects of time, location, and treatment; something that has been infrequently done by investigators examining Markov transitions in a community context (Usher 1979, Facelli and Pickett 1990, Childress et al. 1998, Hill et al. 2002). Hill et al (2002) lament that researchers have resisted using modern tools of loglinear analysis and model selection. I have shown that Markov-type modeling is a reasonable method of analysis for woodpecker tree holes, as the transition predictions were both location and time invariant.

The calculation of damping ratios and the time to return to equilibrium have been used for studies of assemblages prone to frequent catastrophic destruction (e.g. hurricanes, cyclones; Tanner et al. 1994). Other studies using Markov processes to model community succession have found longer half-lives than the 5 months that I predicted in the tree-hole system (coral reefs: 3-6 years, Tanner et al. 1994; intertidal areas: 8.4 months, Wootton 2001b; rocky subtidal: 3-4.2 years, Hill et al. 2002). Given the keystone role that red-cockaded woodpeckers have in the study sites, I do not anticipate that the damping ratio is biologically meaningful in this particular system if all red-cockaded woodpeckers are removed. Without red-cockaded woodpeckers present, tree holes would not be excavated and, hence, the other species would not be able to colonize cluster sites. Previous research has shown that it is extremely difficult to encourage red-cockaded woodpeckers to colonize previously unoccupied sites (Walters et al. 1992). One of the assumptions of the transition matrices presented is that the rate of recruitment and loss of tree holes is constant in this system. Without red-cockaded

woodpeckers to recruit tree holes into the system, there would be no resource available to the assemblage. The implication is that the assemblage can theoretically recover from perturbation in 10 months but this scenario is unlikely if the perturbation involves the reduction of red-cockaded woodpeckers.

The results of the community indices of complexity indicate that complexity increases when red-bellied woodpeckers are removed. Empty tree holes are proportionally equally abundant in both populations (~30%) but the absolute number of empty tree holes is greater in the WRD. The large number of tree holes in the WRD provide more opportunities for species to occupy the tree holes and, hence, greater species richness. As the richness increases, the number of potential species interactions is likely to also increase. By removing red-bellied woodpeckers, it is likely that immigrating individuals cause disruption among the assemblage, thereby increasing potential species turnover rates in tree holes.

An understanding of community-level processes can inform the management of endangered species (Walters 1991) and the relative importance of keystone species (Mills et al. 1993). The approach used in this study demonstrates the usefulness of the application of community-level matrix analysis to endangered species management and studies of the effect of competitors on community dynamics. In previous work, I examined the role of individual behavior (Walters and James unpub ms) and population-level interactions (Walters and James unpub ms) between red-cockaded woodpeckers and red-bellied woodpeckers. This study applies a third approach, the community level. Each of these studies makes the point that the scale at which the investigator approaches studies of competitive interactions can affect interpretations of the nature of the species interactions. At the individual level, most interactions were symmetrical (Walters and James unpub ms). At the population level I showed evidence for both symmetrical interactions and asymmetrical ones where the fitness of red-cockaded woodpeckers was negatively affected by red-bellied woodpeckers in some populations (Walters and James unpub ms). In this study, I show that the dynamics within the assemblage differs between management districts and among treatments. The ARD

population of red-cockaded woodpeckers seemed to be unaffected by the experimental removals of red-bellied woodpeckers but in the WRD, where the population of red-cockaded woodpeckers is undergoing a severe decline, red-cockaded woodpeckers are apparently affected by both red-bellied woodpeckers *and* southern flying squirrels. Application of a community approach allowed me to identify a second source of pressure that potentially could cause the decline of red-cockaded woodpeckers in the WRD. Southern flying squirrels may be exerting similar pressure on red-cockaded woodpeckers in the WRD but direct removal tests of this hypothesis are needed. Southern flying squirrels could interact with red-bellied woodpeckers but have relatively little effect on red-cockaded woodpeckers. Removal of southern flying squirrels in other red-cockaded woodpecker habitats where the former are abundant has yielded mixed results. In one study, red-cockaded woodpeckers had increased reproduction in clusters where flying squirrels were removed (Laves and Loeb 1999) but in another there was no effect of removing flying squirrels (Mitchell et al. 1999).

The findings in this study underscore the importance of comparative studies when evaluating the effect of management programs on endangered species. The dynamics of the assemblage in the declining population of red-cockaded woodpeckers were different from those in the stable population. Despite intense removal efforts, it was not possible to reduce red-bellied woodpecker numbers to measure the effect of sites with and without red-bellied woodpeckers. Instead, removal efforts increased the immigration rate of red-bellied woodpeckers and exacerbated the problem. Interactions that may be important in one management area may not necessarily be so in another. If species are interacting differently among management areas, blanket management policies may not be effective. The WRD, for example, has more tree holes associated with each family group of red-cockaded woodpeckers but the quality and suitability of these tree holes is much less than in the ARD. The effective population size of suitable tree holes is much less in the WRD coupled with the abundance of unused tree holes that promote greater species richness and potential competitive interactions. Managers need to examine the quality of tree holes, not just the quantity. Reasons for the disparity in tree hole number between populations is likely related to past management

policies. By frequently burning forests, dead trees are more likely to be lost and the opportunities for competing members of the assemblage are diminished, as was shown in the ARD. Also, a decrease in burning likely increases hardwood forests, a habitat often used by red-bellied woodpeckers (Shackelford et al. 2000). Forestry practices have also likely contributed to the loss of suitable trees in which to excavate new tree holes. Without suitable trees to excavate, red-cockaded woodpeckers are likely to have higher turnover rates of nesting trees and, hence, a need to create more tree holes over time in areas, like the WRD, with few suitable nesting trees (James et al. 2004).

CONCLUSION

This study demonstrates the value of conducting ecological studies of species interactions using different approaches. In Chapter 1, I determined that, at the individual level, red-cockaded and red-bellied woodpeckers compete symmetrically for tree holes. It was equally likely that a red-cockaded woodpecker would occupy a red-bellied woodpecker tree hole following removal and vice versa. The translocation program used by the United States Forest Service apparently increases the movement within the assemblage. Removal of juvenile red-cockaded woodpeckers induces more red-bellied woodpeckers to move into clusters of red-cockaded woodpecker tree holes.

The occlusion study showed that red-bellied woodpeckers were much more willing to move among tree holes than red-cockaded woodpeckers. Most red-cockaded woodpeckers, when their tree holes were occluded, chose to roost out on a branch rather than use another tree hole. I speculate that the trade-off between the risk of predation by using a tree hole without a protective resin barrier outweighs the risk of roosting outside of a tree hole. When individuals did move, there was an increase in the overall movement of other species occupying tree holes in the cluster.

At the population level (Chapter 2), the results of my long-term studies were mixed. By removing red-bellied woodpeckers, I inadvertently increased the immigration rate of red-bellied woodpeckers into red-cockaded woodpecker clusters. As a result, red-cockaded woodpeckers nested less frequently when red-bellied woodpeckers were removed. Similarly, adult female red-cockaded woodpeckers were more likely to leave the cluster if red-bellied woodpeckers were removed. The removal experiment did not cause any differences in productivity (clutch size or fledging number) of the red-

cockaded woodpeckers. There were at least twice as many red-bellied woodpeckers removed in the population of red-cockaded woodpeckers that is declining. Despite intensive efforts to remove red-bellied woodpeckers, their immigration rate was so high that I was unable to completely remove red-bellied woodpeckers from experimental sites.

At the community level (Chapter 3), I was able to demonstrate that the populations I was examining are close to equilibrium. At that level, red-cockaded woodpeckers are expected to have a proportional abundance close to 40% in the population that is healthy and stable. On the other hand, the prediction is that red-cockaded woodpeckers will only be 24% of the proportional abundance in the declining population. When red-bellied woodpeckers are removed from this declining population, the model predicts that flying squirrel numbers will increase and red-cockaded woodpecker numbers will decrease. The implication is that competition between flying squirrels and red-cockaded woodpeckers is mediated indirectly through red-bellied woodpeckers. Even so, the effect of the removal treatment in the healthy population was minimal. This study provided evidence for some symmetric and some asymmetric interactions between red-cockaded and red-bellied woodpeckers.

Overall, the study shows that the results of experiments designed to analyze how two species interact depends on the level of the approach. Over the short-term, individual behavior was rather symmetrical between the red-cockaded woodpeckers and the red-bellied woodpeckers. Over the longer-term population level, I detected both a negative effect of red-bellied woodpeckers on red-cockaded woodpeckers and a neutral effect. At the community level, I again found mixed results. In the declining population, the relationship between red-bellied woodpeckers and red-cockaded woodpeckers was asymmetric but in the healthy population there was no effect of red-bellied woodpeckers on red-cockaded woodpeckers. Extrapolation of findings among levels without explicit tests can be misleading.

APPENDIX A

Transition probabilities for the control and bimonthly removal sites (N = 11 per treatment) in the Wakulla Ranger District. Species codes are indicated in Table 1. State variables are across the top of each column and Fate variables are listed on the left side of the table.

WRD Control

	RCW	RBW	SFS	EMP	WAT	HIN	BIR
RCW	0.791	0.126	0.072	0.058	0.000	0.045	0.054
RBW	0.133	0.549	0.087	0.173	0.063	0.273	0.135
SFS	0.007	0.037	0.464	0.061	0.109	0.045	0.000
EMP	0.053	0.215	0.130	0.611	0.219	0.455	0.622
WAT	0.003	0.020	0.159	0.052	0.578	0.045	0.027
HIN	0.000	0.020	0.029	0.027	0.000	0.136	0.054
BIR	0.013	0.033	0.058	0.018	0.031	0.000	0.108

WRD Bimonthly Pulse

	RCW	RBW	SFS	EMP	WAT	HIN	BIR
RCW	0.771	0.208	0.020	0.038	0.028	0.000	0.047
RBW	0.110	0.310	0.083	0.129	0.083	0.091	0.093
SFS	0.008	0.060	0.659	0.097	0.111	0.227	0.116
EMP	0.082	0.405	0.151	0.661	0.222	0.545	0.512
WAT	0.016	0.006	0.020	0.018	0.528	0.045	0.023
HIN	0.000	0.006	0.024	0.025	0.028	0.091	0.023
BIR	0.012	0.006	0.044	0.032	0.000	0.000	0.186

APPENDIX B

Transition probabilities for the control, bimonthly, and weekly removal sites (N = 14 per treatment) in the Apalachicola Ranger District. Species codes are indicated in Table 1. State variables are across the top of each column and Fate variables are listed on the left side of the table.

ARD Control

	RCW	RBW	SFS	EMP	WAT	HIN	BIR
RCW	0.828	0.127	0.103	0.125	0.000	0.037	0.100
RBW	0.067	0.589	0.092	0.103	0.043	0.037	0.000
SFS	0.025	0.051	0.540	0.078	0.000	0.074	0.050
EMP	0.077	0.184	0.207	0.584	0.174	0.407	0.750
WAT	0.000	0.006	0.000	0.018	0.739	0.000	0.000
HIN	0.000	0.013	0.057	0.028	0.000	0.444	0.000
BIR	0.002	0.032	0.000	0.064	0.043	0.000	0.100

ARD Bimonthly

	RCW	RBW	SFS	EMP	WAT	HIN	BIR
RCW	0.853	0.219	0.037	0.107	0.000	0.038	0.222
RBW	0.061	0.333	0.062	0.117	0.111	0.077	0.000
SFS	0.010	0.063	0.593	0.047	0.111	0.231	0.222
EMP	0.061	0.333	0.173	0.648	0.111	0.423	0.556
WAT	0.003	0.010	0.012	0.003	0.611	0.000	0.000
HIN	0.000	0.010	0.062	0.044	0.056	0.192	0.000
BIR	0.013	0.031	0.062	0.034	0.000	0.038	0.000

ARD Weekly

	RCW	RBW	SFS	EMP	WAT	HIN	BIR
RCW	0.837	0.263	0.096	0.108	0.026	0.000	0.167
RBW	0.058	0.303	0.036	0.100	0.000	0.048	0.042
SFS	0.013	0.039	0.578	0.081	0.000	0.095	0.208
EMP	0.068	0.342	0.229	0.600	0.132	0.429	0.417
WAT	0.000	0.000	0.024	0.015	0.711	0.095	0.083
HIN	0.003	0.026	0.000	0.027	0.132	0.238	0.042
BIR	0.021	0.026	0.036	0.069	0.000	0.095	0.042

REFERENCES

- Abrams, P.A. (1987) On classifying interactions between populations. *Oecol.*, 73, 272-281.
- Baker, W.W. (1971) Progress report on life history studies of the red-cockaded woodpecker at Tall Timbers Research Station. In: *The ecology and management of the red-cockaded woodpecker* (ed. Thompson RL), pp. 44-59. U.S. Bureau of Sport Fish. and Wildl. and Tall Timbers Res. Sta., Tallahassee, FL
- Beckerman, A.P., Uriarte M. & Schmitz O.J. (1997) Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *P Natl Acad Sci USA*, 94, 10735-10738.
- Beckett, T.A. (1971) A summary of red-cockaded woodpecker observations in South Carolina. In: *The ecology and management of the red-cockaded woodpecker* (ed. Thompson RL), pp. 87-95. U.S. Bureau of Sport Fish. and Wildl. and Tall Timbers Res. Sta., Tallahassee, FL
- Bender, E.A., Case T.J. & Gilpin M.E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology*, 65, 1-13.
- Burnham, K.P. & Anderson D.R. (2002) *Model selection and multimodel inference: a practical information-theoretical approach*. 2nd edn. Springer-Verlag, New York.
- Carter, J.H., Iii, Walters J.R., Everhart S.H. & Doerr P.D. (1989) Restrictors for red-cockaded woodpecker cavities. *Wild. Soc. Bull.*, 17, 68-72.
- Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation*. 2nd edn. Sinauer Associates Inc., Sunderland, MA.
- Chase, J. M., & M. A. Leibold. (2003) *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, IL.
- Childress, W.M., Crisafulli C.M. & Rykiel E.J., Jr. (1998) Comparison of Markovian matrix models of a primary successional plant community. *Ecological Modelling*, 107, 93-102.

- Connell, J.H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: *Ecology and evolution of communities* (eds. Cody ML & Diamond JM), Harvard University Press, Cambridge, MA, pp. 460-490.
- Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Amer. Nat.*, 122, 661-696.
- Conner, R.N. & Locke B.A. (1979) Effects of a prescribed burn on cavity trees of Red-cockaded Woodpeckers. *Wild. Soc. Bull.*, 7, 291-293.
- Conner R.N. & Rudolph D.C. (1995a) Excavation dynamics and use patterns of red-cockaded woodpecker cavities: Relationships with cooperative breeding. In: *Red-cockaded woodpecker: Recovery, ecology and management* (eds. Kulhavy DL, Hooper RG & Costa R), pp. 343-352. Stephen F. Austin State University, Nacogdoches, TX.
- Conner, R.N. & Rudolph D.C. (1995b) Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bull.*, 107, 81-92.
- Conner, R.N. & Rudolph D.C. (1995c) Wind damage to Red-cockaded Woodpecker cavity trees on eastern Texas national forests. In: *Red-cockaded Woodpecker: recovery, ecology and management* (eds. Kulhavy DL, Hooper RG & Costa R), Stephen F. Austin State University, Nacogdoches, TX, pp. 183-190.
- Conner, R.N., Miller O.K. & Adkisson C.S. (1976) Woodpecker dependence on trees infected by fungal heart rot. *Wilson Bull.*, 88, 575-581.
- Conner, R.N., Rudolph D.C. & Walters J.R. (2001) *The red-cockaded woodpecker: surviving in a fire-maintained ecosystem*. University of Texas Press, Austin.
- Conner, R.N., Rudolph D.C., Saenz D. & Schaefer R.R. (1996) Red-cockaded Woodpecker nesting success, forest structure, and southern flying squirrels in Texas. *Wilson Bull.*, 108, 697-711.
- Conner, R.N., Rudolph D.C., Saenz D. & Schaefer R.R. (1997) Species using red-cockaded woodpecker cavities in eastern Texas. *Bull. Texas Ornith. Soc.*, 30, 11-16.
- Conner, R.N., Rudolph D.C., Kulhavy D.L. & Snow A.E. (1991) Causes of mortality of red-cockaded woodpecker cavity trees. *J. Wildl. Manage.*, 55, 531-537.
- Copeyon, C.K., Walters J.R. & Carter J.H., III (1991) Induction of red-cockaded woodpecker group formation by artificial cavity construction. *J. Wildl. Manage.*, 55, 549-556.

- Dhondt, A.A. & Eyckerman R. (1980) Competition between the Great Tit and the Blue Tit outside the breeding season in field experiments. *Ecology*, 61, 1291-1296.
- Enright, N. & Ogden J. (1979) Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Austr. J. Ecol.*, 4, 3-23.
- Facelli, J.M. & Pickett S.T.A. (1990) Markovian chains and the role of history in succession. *Trends Ecol Evol*, 5, 27-30.
- Fingleton, B. (1984) *Models of category counts*. Cambridge University Press, Cambridge.
- Goldberg, D.E. & Barton A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Amer. Nat.*, 139, 771-801.
- Gurevitch, J., Morrow L.L., Wallace A. & Walsh J.S. (1992) A meta-analysis of competition in field-experiments. *Amer. Nat.*, 140, 539-572.
- Harding, S.R. (1997) *The dynamics of cavity excavation and use by the red-cockaded woodpecker (Picoides borealis)*. MS Thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Heard, S.B. (1994) Processing chain ecology: resource condition and interspecific interactions. *J. Anim. Ecol.*, 63, 451-464.
- Hess, C.A. & Costa R. (1995) Augmentation from the Apalachicola National Forest: the development of a new management technique. In: *Red-cockaded Woodpecker: recovery, ecology and management* (eds. Kulhavy DL, Hooper RG & Costa R), Stephen F. Austin State University, Nacogdoches, TX, pp. 385-388.
- Hill, M.F., Witman J.D. & Caswell H. (2002) Spatio-temporal variation in Markov chain models of subtidal community succession. *Ecology Letters*, 5, 665-675.
- Hodge, S. & Arthur W. (1996) Contramensal interactions between species. *Oikos*, 77, 371-375.
- Hooper R.G. (1983) Colony formation by red-cockaded woodpeckers: hypotheses and management implications. In: *Red-cockaded woodpecker symposium II proceedings* (ed. Wood, DA), State of Florida Game and Fresh Water Fish Commission, United States Fish and Wildlife Service, and United States Forest Service. Tallahassee, FL, pp. 72-77.
- Hooper, R.G. & Lennartz M.R. (1983) Roosting behavior of Red-cockaded woodpecker clans with insufficient cavities. *J. Field Ornithol.*, 54, 72-76.

- Horn, H.S. (1975) Markovian properties of forest succession. In: *Ecology and evolution of communities* (eds. Cody ML & Diamond JM), Harvard University Press, Cambridge, MA, pp. 196-211.
- Hovis, J.A. & Labisky R.F. (1985) Vegetative associations of Red-cockaded Woodpecker colonies in Florida. *Wild. Soc. Bull.*, 13, 307-314.
- Jackson, J.A. (1977) Red-cockaded woodpeckers and pine red heart disease. *Auk*, 94, 160-163.
- Jackson, J.A. (1978) Competition for cavities and red-cockaded woodpecker management. In: *Endangered Birds: Management techniques for preserving threatened species* (ed. Temple SA), University of Wisconsin Press, Madison, WI, pp. 103-112.
- James, F.C., Hess C.A. & Kufirin D. (1997) Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. *Ecol. Appl.*, 7, 118-129.
- James, F.C., Hess C.A., Kicklighter B.C. & Thum R.A. (2001) Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. *Ecol. Appl.*, 11, 854-870.
- James, F.C., Richards P.M., Hesslein R.H., McCluney K.E., Walters E.L. & Schrader M.S. (2004) Sustainable forestry for the red-cockaded woodpecker's ecosystem. In: *Red-cockaded woodpecker: road to recovery* (eds. Costa R & Daniels SJ), Hancock House Publishers, Blaine, WA, pp. In Press.
- Kappes, J.J. (1997) Defining cavity-associated interactions between red-cockaded woodpeckers and other cavity-dependent species: Interspecific competition or cavity kleptoparasitism? *Auk*, 114, 778-780.
- Kappes, J.J., Jr. & Harris L.D. (1995) Interspecific competition for red-cockaded woodpecker cavities in the Apalachicola National Forest. In: *Red-cockaded woodpecker: recovery, ecology and management* (eds. Kulhavy DL, Hooper RG & Costa R), Stephen F. Austin State University, Nacogdoches, TX, pp. 389-393.
- Korotkov, V.N., Logofet D.O. & Loreau M. (2001) Succession in mixed boreal forest of Russia: Markov models and non-Markov effects. *Ecological Modelling*, 142, 25-38.
- Laska, M.S. & Wootton J.T. (1998) Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79, 461-476.
- Laves, K.S. & Loeb S.C. (1999) Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker *Picoides borealis* reproductive success. *Animal Conservation*, 2, 295-303.

- Lay, D.W. & Russell D.N. (1970) Notes on the Red-cockaded Woodpecker in Texas. *Auk*, 87, 781-786.
- Lennartz, M.R., Hooper R.G. & Harlow R.F. (1987) Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. *Behav. Ecol. Sociobiol.*, 20, 77-88.
- Levins, R. (1968) *Evolution in changing environments: some theoretical explorations*. Princeton University Press, Princeton, NJ.
- Ligon, J.D. (1970) Behavior and breeding biology of the Red-cockaded Woodpecker. *Auk*, 87, 255-278.
- Ligon, J.D. (1971) Some factors influencing numbers of the red-cockaded woodpecker. In: *The ecology and management of the red-cockaded woodpecker* (ed. Thompson RL), pp. 30-43. U.S. Bureau of Sport Fish. and Wildl., and Tall Timbers Res. Sta., Tallahassee, FL
- Łomnicki, A. (1988) *Population ecology of individuals*. Princeton University Press. Princeton, NJ
- Lough, T.J., Wilson J.B., Mark A.F. & Evans A.C. (1987) Succession in a New Zealand alpine cushion community: a Markovian model. *Veget.*, 71, 129-138.
- MacArthur, R. (1972) Strong, or weak, interactions? *Trans. Connect. Acad. Arts Sci.*, 44, 177-188.
- Martin, T.E. (1986) Competition in breeding birds: on the importance of considering processes at the level of the individual. In: *Current Ornithology* (ed. Johnston RF), Plenum Press, New York, NY, pp. 181-210.
- May, R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413-414.
- McAuliffe, J.R. (1988) Markovian dynamics of simple and complex desert plant communities. *Amer. Nat.*, 131, 459-490.
- Miller, T.E. & Kerfoot W.C. (1987) Redefining indirect effects. In: *Predation: direct and indirect impacts on aquatic communities* (eds. Kerfoot WC & Sih A), University Press of New England, Hanover, NH, pp. 33-37.
- Mills, L.S., Soulé M.E. & Doak D.F. (1993) The keystone-species concept in ecology and conservation. *BioScience*, 43, 219-224.
- Mitchell, L.R., Carlile L.D. & Chandler C.R. (1999) Effects of southern flying squirrels on nest success of Red-cockaded Woodpeckers. *J. Wildl. Manage.*, 63, 538-545.

- Moloney, K.A. (1988) Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology*, 69, 1588-1598.
- Neal, J.C., Montague W.G. & James D.A. (1992) Sequential occupation of cavities by red-cockaded woodpeckers and red-bellied woodpeckers in the Ouachita National Forest. *Arkansas Academy of Science*, 46, 106-108.
- Newton, I. (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Cons.*, 70, 265-276.
- Rego, F., Pereira J. & Trabaud L. (1993) Modelling community dynamics of a *Quercus coccifera* L. garrigue in relation to fire using Markov chains. *Ecological Modelling*, 66, 251-260.
- Relyea, R.A. & Yurewicz K.L. (2002) Predicting community outcomes from pairwise interactions: integrating density- and trait-mediated effects. *Oecol.*, 131, 569-579.
- Rudolph, D.C. & Conner R.N. (1991) Cavity tree selection by red-cockaded woodpeckers in relation to tree age. *Wilson Bull.*, 103, 458-467.
- Rudolph, D.C., Conner R.N. & Turner J. (1990) Competition for red-cockaded woodpecker roost and nest cavities: effects of resin age and entrance diameter. *Wilson Bull.*, 102, 23-36.
- Schoener, T.W. (1974a) Resource partitioning in ecological communities. *Science*, 185, 27-39.
- Schoener, T.W. (1974b) Some methods for calculating competition coefficients from resource-utilization spectra. *Amer. Nat.*, 108, 332-340.
- Schoener, T.W. (1983) Field experiments on interspecific competition. *Amer. Nat.*, 122, 240-285.
- Schrader, M.S., Walters E.L., James F.C. & Greiner E.C. (2003) Seasonal prevalence of a haematozoan parasite of red-bellied woodpeckers (*Melanerpes carolinus*) and its association with host condition and overwinter survival. *Auk*, 120, 130-137.
- Shackelford, C. E., Brown, R. E. & Connor, R.N. (2000) Red-bellied woodpecker (*Melanerpes carolinus*): In: *The birds of North America*, No. 500, (eds. Poole A & Gill F), The Birds of North America, Philadelphia, PA, pp. 1-24.
- Sih, A., Crowley P., Mcpeek M., Petranka J. & Strohmeier K. (1985) Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.*, 16, 269-311.
- SPSS Inc. (2000) *SPSS Version 10.0 for Windows*. SPSS Inc., Chicago, IL

- StatSoft, Inc. (2000). *STATISTICA for Windows*. StatSoft, Inc., Tulsa, OK.
- Sutherland, W.J. (1996) *From individual behaviour to population ecology*. Oxford University Press, New York.
- Tanner, J.E., Hughes T.P. & Connell J.H. (1994) Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology*, 75, 2204-2219.
- Temeles, E.J. (1994) The role of neighbors in territorial systems: when are they 'dear enemies'? *Anim. Behav.*, 47, 339-350.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1987) The importance of the mechanisms of interspecific competition. *Amer. Nat.*, 129, 769-774.
- U.S. Fish and Wildlife Service (2003) *Recovery plan for the red-cockaded woodpecker (picoides borealis): Second revision*. U.S. Fish and Wildlife Service, Atlanta, GA.
- Usher, M.B. (1979) Markovian approaches to ecological succession. *J. Anim. Ecol.*, 48, 413-426.
- Waggoner, P.E. & Stephens G.R. (1970) Transition probabilities for a forest. *Nature*, 225, 1160-1161.
- Walters, E.L. & Kneitel J.M. (2004) Use of water-filled red-cockaded woodpecker cavities by other organisms. In: *Red-cockaded woodpecker: road to recovery* (eds. Costa R & Daniels SJ), Hancock House Publishers, Blaine, WA, pp. In press.
- Walters, J.R. (1991) Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Ann. Rev. Ecol. Syst.*, 22, 505-523.
- Walters, J.R., Copeyon C.K. & Carter J.H., III (1992) Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk*, 109, 90-97.
- Walters, J.R., Doerr P.D. & Carter J.H., III (1988) The cooperative breeding system of the red-cockaded woodpecker. *Ethology*, 78, 275-305.
- Werner, E.E. (1992) Individual behavior and higher-order species interactions. *Amer. Nat.*, 140, S5-S32.
- Werner, E.E. & Anholt B.R. (1996) Predator-induced behavioral indirect effects: Consequences to competitive interactions in anuran larvae. *Ecology*, 77, 157-169.

Wootton, J.T. (2001a) Causes of species diversity differences: a comparative analysis of Markov models. *Ecology Letters*, 4, 46-56.

Wootton, J.T. (2001b) Prediction in complex communities: analysis of empirically derived Markov models. *Ecology*, 82, 580-598.

Yeaton, R.I. & Bond W.J. (1991) Competition between two shrub species: dispersal differences and fire promote coexistence. *Amer. Nat.*, 138, 328-341.

Zack, S. & Stutchbury B.J. (1992) Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behav.*, 123, 194-219.

BIOGRAPHICAL SKETCH

Eric L. Walters

Education and Degrees

Doctor of Philosophy

Florida State University (Tallahassee, Florida) Spring 2004

Master of Science

University of Victoria (Victoria, British Columbia) Fall 1997

Bachelor of Science

University of Victoria (Victoria, British Columbia) Spring 1990

Fellowships and Awards

Robert B. Short Zoology Scholarship (\$2,000) - 2000

Allen Broussard Conservation Consolation Scholarship (\$50) - 1999 - 2000

Florida State University Dissertation Research Grant (\$500) - 1999 - 2000

North American Bluebird Society Research Award (\$1,000) - 1999 - 2000

King-Platt Fellowship - University of Victoria (\$26,000) - 1994 – 1996

Best Natural History Talk - University of Victoria Graduate Symposium - 1994

University of Victoria Graduate Teaching Fellowship (\$1,000) – 1993 - 1994

King-Platt Memorial Scholarship - University of Victoria (\$3,000) – 1993 - 1994

Best Teaching Assistant – Biology Department, University of Victoria – 1993

Professional Societies

American Association for the Advancement of Science

American Ornithologists' Union

American Society of Naturalists

Association of Field Ornithologists

Cooper Ornithological Society

Ecological Society of America

Florida Ornithological Society

Society of Canadian Ornithologists

Wilson Ornithological Society

Meetings / Seminars

Presentations of papers / posters at meetings and invited seminars

2003, November, Dartmouth College, Hanover, NH

2003, June, UC Berkeley (Hastings Reservation), Carmel Valley, CA

2003, January, Red-cockaded Woodpecker Symposium IV, Savannah, GA

2002, August, Ecological Society of America, Tucson, AZ

2001, October, Western Energy Institute and Northwest Public Power Association, NV

2001, August, Ecological Society of America, Madison, WI

2000, November, FSU Ecology and Evolution Seminar Series, Tallahassee, FL

2000, October, Northeast Pole Conference, Binghamton, NY

1998, August, Ecological Society of America, Baltimore, MD

1997, August, American Ornithologists' Union, Minneapolis, MN

1997, May, Electric Power Research Institute, Charlotte, NC

1997, April, Florida Ornithological Society, Wakulla Springs, Florida

1997, February, Tallahassee Ornithological Society, Tallahassee, Florida

1994, March, Pacific Ecology Conference, Bamfield, British Columbia

1994, March, Graduate Student Symposium, Victoria, British Columbia

Referee Activities

Auk, BioScience, Canadian Journal of Forest Research, Condor, Florida Field Naturalist, Journal of Field Ornithology, Journal of Wildlife Management

Publications

Walters, E.L. and J.M. Kneitel. 2004. Use of water-filled red-cockaded woodpecker cavities by other organisms. *in*: Costa, R. and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers. Blaine, Washington. In Press.

James, F.C., Richards, P., Hess, C.A., McCluney, K.E., Walters, E.L., and M.S. Schrader. 2004. Sustainable forestry for the red-cockaded woodpecker's ecosystem. *in*: Costa, R. and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers. Blaine, Washington. In Press.

Schrader, M.S., E.L. Walters, F.C. James and E.C. Greiner. 2003. Seasonal prevalence of a haematozoan parasite of the Red-bellied Woodpecker (*Melanerpes carolinus*) and its association with host condition and overwinter survival. AUK 120:130-137.

Walters, E.L., E.H. Miller, and P.E. Lowther. 2002. Yellow-bellied Sapsucker (*Sphyrapicus varius*). *In* The Birds of North America, no. 662. (A. Poole and F. Gill, eds). The Birds of North America, Inc. Philadelphia, PA.

Walters, E.L., E.H. Miller, and P.E. Lowther. 2002. Red-breasted Sapsucker (*Sphyrapicus ruber*) and Red-naped Sapsucker (*Sphyrapicus nuchalis*). *In* The Birds of North America, no. 663. (A. Poole and F. Gill, eds). The Birds of North America, Inc. Philadelphia, PA.

Foster, G.W., J.M. Kinsella, E.L. Walters, M.S. Schrader, and D.J. Forrester. 2002. Parasitic helminths of red-bellied woodpeckers (*Melanerpes carolinus*) from the Apalachicola National Forest in Florida. *Journal of Parasitology*. 88:1140-1142.

Walters, E.L. 2002. Book Review: Birds of British Columbia, Volume 4 – Wood-Warblers through Old World Sparrows. *Auk* 119:293-295.

Harding, E.K., E.E. Crone, B.D. Elder, J.M. Hoekstra, A.J. McKerrow, J.D. Perrine, J. Regetz, L.J. Rissler, A.G. Stanley, E.L. Walters*, and NCEAS HCP Working Group. 2001. The scientific foundations of habitat conservation plans: a quantitative assessment. *Conservation Biology*. 15:488-500 (*order of authors alphabetical after lead author)

Walters, E.L. and E.H. Miller. 2001. Predation on woodpeckers in British Columbia. *Canadian Field-Naturalist* 115(3): 411-419.

Miller, E.H., E.L. Walters and H. Ouellet. 1999. Plumage, size, and sexual dimorphism in the Queen Charlotte Islands Hairy Woodpecker, *Condor* 101:86-95.

Walters, E.L. 1996. Habitat and space use of the Red-naped Sapsucker, *Sphyrapicus nuchalis*, in the Hat Creek valley, south-central British Columbia. MS Thesis, University of Victoria, Victoria, British Columbia. 98p.

Baird, R.W., Walters, E.L. and P.J. Stacey. 1993. Status of the Bottlenose Dolphin, *Tursiops truncatus*, in Canada. *Canadian Field-Naturalist* 107(4):466-480.