Effects of Military Training Activity on
Red-cockaded Woodpecker Demography and Behavior

and

New Territory Formation in the
Cooperatively Breeding Red-cockaded Woodpecker

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Abstract

The red-cockaded woodpecker (*Picoides borealis*) is a federally endangered species. As such, populations need to be increased in order to achieve recovery goals outlined by the U.S. Fish and Wildlife Service. My thesis is composed of two chapters that represent opposite sides of this issue. The first chapter investigates whether military training activity negatively affects red-cockaded woodpeckers. Military installations in the southeastern United States contain several of the largest remaining red-cockaded woodpecker populations. Six of the 15 installations harboring these birds are designated primary core populations; thus, population increases on these sites are critical to recovery of the species. However, restrictions on military training activity associated with red-cockaded woodpecker protection are a cause of concern on military installations that sometimes constrains management for population growth. Current restrictions are based on assumptions of potential impacts rather than scientific evidence, so we evaluated two different restriction regimes to test for training activity effects. The second chapter concerns how to induce populations to grow more rapidly through natural processes. As a cooperative breeder, red-cockaded woodpeckers preferentially compete for existing breeding positions and queue in the form of helping or floating to obtain a breeding vacancy, rather than create new territories. I used 20 years of demographic data collected as part of a long-term monitoring study of red-cockaded woodpeckers to investigate mechanisms that stimulate territory creation in this cooperatively breeding species.

Dedication

To Susan J. Daniels, a friend for too short a time, but who continues to be an inspiration.

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CHAPTER 1: EFFECTS OF MILITARY TRAINING ACTIVITY ON RED-COCKADED WOODPECKER DEMOGRAPHY AND BEHAVIOR

ABSTRACT

Military installations in the southeastern United States contain several of the largest remaining red-cockaded woodpecker populations. Six of the 15 installations harboring these birds are designated primary core populations; thus, population increases determined by the U.S. Fish and Wildlife Service are necessary for recovery of the species. However, restrictions on military training activity associated with red-cockaded woodpecker protection are a cause of concern on military installations that sometimes constrains management for population growth. Current restrictions are based on assumptions of potential impacts rather than scientific evidence of such impacts, so we evaluated two different restriction regimes to test for training activity effects. From 2001 through 2005 we designated 19 red-cockaded woodpecker clusters as controls, which were subject to current military training activity restrictions, and 19 clusters as experimental, having no restrictions. Control clusters averaged significantly longer incubation bouts but suffered significantly higher rates of partial brood loss. We found no significant difference between treatments in 13 other demographic and behavioral measures. While our results suggest that red-cockaded woodpeckers can habituate to military training activity, we were unable to adequately assess the extent to which differences in restrictions resulted in differences in training activity within clusters. Therefore, it would be premature to extrapolate our findings to a base-wide, unrestricted training regime.

INTRODUCTION

Multiple-use lands are increasingly important for the conservation of biological diversity as human population and concomitant development leave little room for pristine lands. In addition to less tangible benefits, conserving biodiversity helps ensure ecosystem integrity, further sustaining human enterprise (Ripley and Leslie 1997; see Callicott [1997] for a comprehensive discussion of values in conserving biodiversity). Because there is a growing need to integrate management of multiple land uses, including species and ecosystem conservation as well as human consumptive purposes (Hansen et al. 1993), many state and

federal agencies employ multiple-use management strategies, which include threatened and endangered species management.

The United States Department of Defense (DoD) is responsible for managing more than 25 million acres, which comprises only 3% of the total federal land base. However, DoD lands harbor higher densities of threatened and endangered species than lands managed by the Bureau of Land Management, U.S. Forest Service, U.S. Fish and Wildlife Service, and National Park Service (Ripley and Leslie 1997). Thus, military installations have a disproportionately high number of federally threatened and endangered species (Leslie et al. 1996). This discrepancy is partially due to the location of installations in a diverse array of habitat types to access a wide range of training environments (Ripley and Leslie 1997, Tazik and Martin 2002). While natural landscapes are necessary for training realism and combat readiness, management for threatened and endangered species often prescribes restrictions that may impede or alter training exercises. Therefore, potential conflicts exist between management for threatened and endangered species and the military's ability to effectively and realistically train.

Effects of military training activity, however, have not been well established for any species. Most existing literature concerns effects of aircraft noise on wildlife (for a review see Larkin et al. 1996). Few studies have conducted experimental manipulations (Larkin et al. 1996), and even fewer have attempted to quantify long-term, population-level impacts of military training activity (but see Anderson et al. 1989 and Palmer et al. 2003).

Much of the literature concerning military training activity and avian species has focused on short-term behavior changes, which may or may not contribute to population-level effects. Ward et al. (1999) compared responses of fall-staging Pacific brant (*Branta bernicla nigricans*) and Canada geese (*B. canadensis*) to aircraft overflights; while 75% of brant flew in response to aircraft, only 9% of Canada geese reacted. Conomy et al. (1998*b*) subjected American black ducks (*Anas rubripes*) and wood ducks (*Aix sponsa*) to actual and simulated jet aircraft activity during a field experiment with captive birds. While both species initially responded to the disturbance, black ducks appeared to habituate over a period of several days while wood ducks did not. Thus, it seems that there is little utility in attempting to generalize across species.

Additionally, while the majority of studies found little effect of aircraft disturbance on bird behavior, more population-relevant measures have not been considered (Conomy et al. 1998*a,b*; Delaney et al. 1999; Ward et al. 1999; Goudie and Jones 2004; but see Palmer et al.

2003). Minimal behavioral responses do not preclude increased heart rate and hormonal changes due to stress that could affect productivity and/or survival. In this study we attempt to experimentally quantify short-term behavior and long-term demographic effects of military training on red-cockaded woodpeckers (*Picoides borealis*) by manipulating training activity restrictions.

The Red-cockaded woodpecker

Life History.— The red-cockaded woodpecker is a federally endangered species, endemic to open, mature pine forests of the southeastern United States. It is unique among North American cavity nesters because it constructs roost and nest cavities in live pine trees (USFWS 1985). Cavity excavation may take several years due to the difficulty of construction in live pines (Jackson et al. 1979; Harding and Walters 2002, 2004), which has caused cavities to be an unusually variable, critical resource that may have promoted the evolution of cooperative breeding in red-cockaded woodpeckers (Walters et al. 1992). Cavity construction in live pine trees also requires large, mature trees containing sufficient heartwood diameter to ensure that the cavity chamber does not breach the sapwood (Jackson et al. 1979). Rather than construct cavities in unoccupied habitat, red-cockaded woodpeckers compete intensely for territories with existing cavities (Walters 1990, Walters 1991, Walters et al. 1992), with the natural creation of new territories being quite rare (Hooper 1983, Walters 1990).

Intensive logging of longleaf pine (*Pinus palustris*) forests in the 1800s and 1900s, with which red-cockaded woodpeckers are strongly associated, resulted in extensive habitat loss that endangered this species (Conner et al. 2001). Red-cockaded woodpeckers have been further threatened by habitat degradation. The longleaf pine ecosystem is dependent on frequent (1-5 years), low-intensity fires to maintain an open midstory. Fire suppression policies have allowed scrub oak species (*Quercus* spp.) to reach the midstory, causing red-cockaded woodpeckers to abandon their cavities (Conner and Rudolph 1989). Selective logging of large, mature pine trees – necessary for cavity construction – in remaining longleaf pine forests has further endangered red-cockaded woodpecker populations.

Red-cockaded woodpeckers are cooperative breeders, living in groups that typically contain a breeding pair and 0-4 adult, non-breeding helpers, which are usually male offspring from previous years (Lennartz et al. 1987, Walters et al. 1988, Walters 1990). Each individual

roosts singly in a cavity, with cavity trees generally spatially clumped (Walters 1990). The group defends this collection of cavity trees, termed a cluster, against intruders.

Red-cockaded woodpecker population dynamics are unusual because male helpers act as a buffer with respect to natality and mortality. Helpers rapidly occupy breeding vacancies when mortality outweighs reproduction, while helper class numbers grow when births exceed deaths (Walters 1991, Heppell et al. 1994). Thus, the number of breeding pairs varies little across years. Conversely, because cavities are a limiting resource and an essential component of high quality territories, cavity tree dynamics have a substantial impact on population demography (Walters et al. 1992). Therefore, population dynamics are primarily determined by the availability of suitable territories – i.e. habitat containing cavity trees (USFWS 2003).

Artificial cavity construction has been employed since 1989 to stabilize declining populations and stimulate population growth (Conner et al. 2001). Cavity provisioning involves the placement of artificial cavities via drilling cavities (Copeyon 1990) or inserting preformed boxes (Allen 1991) into live pine trees. Both techniques address the lengthy process of natural cavity construction and the rarity with which new territories are created. Preformed boxes also allow placement of artificial cavities in smaller pines thereby addressing the lack of larger trees in remaining habitat (Allen 1991). Artificial cavities installed in previously unoccupied suitable habitat are termed recruitment clusters and are readily occupied (Walters et al. 1992).

On Military Lands.— The red-cockaded woodpecker illustrates the potential conflict between endangered species management and military training. Military installations contain several of the largest remaining red-cockaded woodpecker populations. Six of the 15 installations that harbor red-cockaded woodpeckers are designated primary core populations necessary for the recovery of the species (USFWS 2003). These military lands need not only maintain their existing populations but also increase them to meet recovery objectives.

Although training activity has not been reduced on most installations, it has been significantly altered due to red-cockaded woodpecker management (Conner et al. 2001). Many installations are willing to cooperate with training activity restrictions applied to their existing populations but are wary of increasing them for fear of further constraints (Conner et al. 2001). Further, current restrictions are based on assumptions of potential impacts rather than scientific evidence of these impacts. Disturbance from military training activities could potentially affect

survival and reproduction, as well as alter reproductive and non-reproductive behaviors such as incubation and nestling provisioning rates, roosting times, and breeder turnover.

Only three studies of military training activity impacts on red-cockaded woodpeckers have been undertaken. A study conducted on Fort Bragg army installation in south-central North Carolina found reduced nest success, clutch size, and number of fledglings, and increased male breeder turnover in clusters near bivouac and landing zones (Mobley et al. 1995). They also observed smaller clutch sizes and increased female breeder turnover in clusters near weapons impact areas. However, all clusters in the study area were subject to the same training activity restrictions, and although some assessment was possible by comparing actual training levels, the study was limited by its correlative approach. A preliminary study on Camp Lejeune, a Marine Corps base with similar training activities to Fort Bragg, examined nestling provisioning rates in response to noise simulators (Walters 2001). Responses among groups were highly variable, ranging from strongly inhibited to unaffected. Another army installation, Fort Benning, located in west-central Georgia, analyzed military training activity impacts on reproductive measures by comparing recorded noise and vibration levels at clusters experiencing frequent military training activity with clusters that were relatively undisturbed (Doresky et al. 2001). Training activity did not significantly affect clutch size, brood size, number of adults, provisioning rates, or nestling and adult mass in this correlative analysis. However, the study also failed to find significant differences in the amount of noise or vibration levels between control and treatment clusters. Taken together, the evidence presented in these three studies that disturbance from military training activity affects the demography or behavior of red-cockaded woodpeckers is equivocal.

Conner et al. (2001) speculate that disturbances that impact survival and productivity will not have population-level effects on red-cockaded woodpeckers because of the buffering effect of helpers discussed above. Ultimately, however, the helper class is finite. If disturbance from military training activities is sufficiently disruptive, the helper-class buffer could be depleted by lowered reproduction and increased mortality, thus altering population dynamics. Also, female helpers rarely occur and thus availability of breeding females has little buffer. Therefore, our study evaluated the effects of military training activities on both short-term behavior and long-term demographics of red-cockaded woodpeckers.

STUDY AREA

Marine Corps Base Camp Lejeune is located in Onslow County along the central coast of North Carolina. The Main Base is comprised of 61,110 ha, 10,522 of which is open water (Convery 2002). Most of the red-cockaded woodpecker groups are associated with longleaf pine. For a more detailed description, including habitat types and frequency see Zwicker and Walters (1999).

All red-cockaded woodpecker groups occur on the Main Base. The Greater Sandy Run Area, 16,593 ha, was purchased in 1992 and is adjacent to and southwest of the Main Base; it contains no red-cockaded woodpecker groups (Fig. 1). The eastern portion of the Main Base is effectively separated from the western portion by Stones Bay and the New River. Most red-cockaded woodpecker groups are found in the Combat Town and Northeast training areas and the G-10 impact area, located in the eastern portion (Fig. 1). A smaller subpopulation, the Verona Loop Training Area, is located in the western portion. Dispersal between the Northeast training area, Combat Town training area, and the G-10 impact area is frequent, whereas dispersal between the eastern and western subpopulations is rare.

Marine Corps Base Camp Lejeune is designated a primary core population for red-cockaded woodpeckers (USFWS 2003). A diverse array of military training activities are conducted over the entire base, including rotary and fixed wing aircraft; tracked and wheeled vehicles, foot traffic, and weapons firing with more than 50 live-fire ranges, 34 artillery gun positions, seven mortar positions, and three impact areas (EMD 1999). Military training activity restrictions within a 200-foot buffer of a red-cockaded woodpecker cluster exclude vehicular traffic, bivouacking, foxhole digging, the establishment of any fixed position, girdling trees with wire, and burying cable (EMD 1999). Additionally, artillery firing is prohibited within 600 feet of the cluster, as is anything producing excessive disturbance, such as noise simulators or smoke.

METHODS

Study Design

Our study design served two purposes: first, it allowed the red-cockaded woodpecker population on Camp Lejeune to increase without a proportional increase in military training activity restrictions, easing concerns of military trainers; second, it provided an opportunity to

directly compare the effects of alternative military training restriction levels on red-cockaded woodpeckers. We provided twice the number of recruitment clusters required by Camp Lejeune's Red-cockaded woodpecker Management Plan (EMD 1999), with only half of these new clusters subjected to the training activity restrictions just described (control treatment). Clusters without any military training activity restrictions were designated as the experimental treatment. Two other types of clusters were also included in both control and experimental treatments: new clusters naturally created by red-cockaded woodpeckers and several existing natural clusters (approved by the U.S. Fish and Wildlife Service to be included in this study for research purposes). We assigned clusters to control and experimental treatments separately by type. Within each type (recruitment, natural new, natural existing), we paired clusters – one each from the control and experimental treatments – by similar habitat. Our sample size increased throughout our study because we provided new recruitment clusters during the first three years and the woodpeckers created several new clusters. Thus, we assigned a total of 19 clusters to the control treatment and 19 clusters to the experimental treatment.

We deemed the 45 existing clusters not included in the experimental or control treatments as reference clusters. Reference clusters were older, established clusters and contained larger group sizes and older breeders, both of which are positively correlated with reproductive measures (Lennartz et al. 1987, Walters 1990). We chose new clusters (recruitment, natural new, and natural existing) for our experiment because they typically contain smaller group sizes and younger breeders, thus omitting some of the variation inherent to a larger range of both group sizes and breeder ages found in reference clusters. However, we included reference clusters in correlation analyses because this wider range of variation would better reflect the relationships between group size, breeder age, and reproductive measures. We also chose new clusters for logistic reasons: (1) obtaining approval to remove restrictions on the three existing natural clusters for our experimental treatment was difficult; and (2) comparing established restricted clusters to new experimental clusters would not have been an objective study design. We also included reference clusters in selected graphs for comparison purposes; reference clusters are like control clusters because military training activity is restricted in both. We used reference clusters in correlation analyses and for graphical comparison purposes only; they were not included in any analyses to test for military training activity effects.

Data Collection

Two types of data were collected from 2000 through 2005: (1) demographic data collected during annual breeding season monitoring (see Walters et al. [1988] for a detailed description of breeding season monitoring); and (2) behavioral observations, which consisted of roost surveys, incubation surveys, and nestling provisioning surveys.

Demographic Measures.— We compared the following demographic measures between clusters with military training activity restrictions (control) and clusters without any training activity restrictions (experimental) to assess disturbance effects on red-cockaded woodpeckers: (1) whether a recruitment cluster was occupied within 2 years of availability (yes or no); (2) whether a cluster was occupied (yes or no); (3) whether a cluster was occupied by a potential breeding group – at least one male and one female inhabiting a cluster (yes or no); (4) nesting effort – whether a group nested (yes or no); (5) nest failure – whether a nest failed (yes or no); (6) clutch size – total number of eggs laid; (7) partial brood loss – the proportion of eggs that did not survive to fledging, exclusive of whole brood loss (proportion of eggs lost = 1); (8) number of fledglings produced per successful nest (i.e., nests that produced at least one fledgling; (9) number of fledglings produced per potential breeding group – analyzed in addition to 8 to provide an overall measure of productivity (Daniels and Walters 2000*b*); (10) breeder turnover – whether a breeding individual relocated to another cluster between breeding seasons (yes or no); and (11) mortality – whether an individual perished between breeding seasons (yes or no).

We included potential breeding groups, solitary males, captured clusters, and inactive clusters in our dataset to analyze whether a cluster was occupied. A captured cluster is one that is only used for roosting by at least one bird belonging to another group that already has a primary cluster. While a captured cluster's status is occupied, the number of adults associated with it is 0. To assess clusters occupied by a potential breeding group, our data subset included only occupied clusters, not all clusters. For the analysis of nesting effort, our data subset included clusters occupied by a potential breeding group, not all occupied clusters. We analyzed measures 4 through 8 to determine if training activity effects occurred at different stages of the nesting cycle.

We included only first nesting attempts in analyses 5-9. We included birds of unknown age in our datasets for analyses 10 and 11, as well as our correlation analyses, to increase sample size. These individuals were assumed to be the minimum age; for example, an after-second-year

(ASY) individual was considered a third-year (i.e., two-year-old) bird (Daniels and Walters 2000*a,b*). We believe this reasonable considering few birds disperse long distances (median distance 1.0-4.5km, depending on sex and status; Walters et al. 1988), the nearest population to Camp Lejeune is banded (Croatan National Forest), and the percent of missed nests per year (yielding unbanded fledglings) is quite low using the census methods described in Walters et al. (1988). Thus, unknown-aged adults are likely fledglings from nests missed the year prior to banding.

Behavioral Surveys.— We conducted roost surveys for all occupied clusters once per month from October through April. Surveys were conducted for one hour and performed to cover the latest possible time a bird would roost at night, to avoid inaccurately documenting a bird as open-roosting (not roosting in a cavity). We recorded each individual's roost time and whether it roosted in a cavity tree.

We conducted two incubation surveys for all nesting groups for one hour each on different days during the incubation period, one each in the morning and afternoon. We initiated incubation surveys immediately after clutch completion and used prior nest check information to project the hatch date (or earliest hatch date possible) to avoid missing a survey. We recorded times on and off the nest for individual incubation bouts.

We conducted four nestling provisioning surveys for one hour each on four different days during the nestling period, two each in the morning and afternoon. We alternated surveys in terms of morning or afternoon and separated them in time to the extent permitted by military training. We began provisioning surveys after three days post-hatch because adults mostly brood rather than feed nestlings prior to this time period. We observed nests in both the morning and afternoon because Khan and Walters (2002) found that provisioning rates varied by time of day. Further, we performed at least one survey before nestlings were ten days old because it is unknown whether adults provision more or less often or the same amount prior to this age. We classified time of day as 'morning' (until 1200 hours) or 'afternoon' (after 1200 hours) and nestling age as 'young' (less than 10 days old) or 'old'. We recorded the total number of visits made to the nest cavity by all individuals in a group.

Data Analyses

Demographic Measures.— We used repeated measures analysis of covariance to examine military training activity effects on clutch size, partial brood loss, number of fledglings

per successful nest, and number of fledglings per potential breeding group. We used simple logistic regression to analyze whether a recruitment cluster was occupied within two years of availability (measure 1), and repeated measures logistic regression to analyze all other demographic measures. Except for measure 1, military training activity (control, experimental) and year were fixed, independent variables and cluster pairing based on habitat was included as a random blocking factor in all models; military training activity was our only (independent) variable for measure 1.

We analyzed breeder turnover separately by sex because males rarely move once they have acquired a territory (Walters et al. 1988). Mortality was also examined separately for each sex, and further separated by status (fledgling, helper, breeder, etc.) since mortality varies by these characteristics (Walters et al. 1988). Therefore, we tested nine categories for a difference in mortality due to military training activity: female breeders, helpers, fledglings, and floaters; and male breeders, helpers, fledglings, floaters, and solitary males. Floaters are individuals not associated with a particular cluster; solitary males reside in a cluster but have no mate. Group size was included in our models for breeder mortality because Khan and Walters (2002) documented enhanced breeder survival with increased group size.

We used correlation analyses of measures 4 through 11 with group size, male breeder age, and female breeder age to determine potential covariates because all are correlated with productivity (Lennartz et al. 1987, Walters 1990). Due to small sample sizes, we included only the one covariate that had the strongest significant correlation to avoid parsing out too many degrees of freedom. We investigated correlations among five different groups: all clusters pooled together, control and experimental clusters pooled together, and reference, control, and experimental clusters separately.

Behavioral Surveys.— We tested for military training activity effects on roosting times using doubly repeated measures analysis of covariance (repeated measures occurred in two dimensions – month and year). We calculated the monthly mean number of minutes before sunset that individuals in a cluster roosted for our dependent variable. We obtained time of sunset from online U.S. Naval Observatory records for Camp Lejeune (http://www.usno.navy.mil/). Treatment and month were our independent variables, and year was included in the model as a random blocking factor. We included month in our model because we suspected temperature might affect roost times.

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We used doubly repeated measures analysis of covariance to evaluate treatment effects on the total length of time spent incubating by all individuals in a group and the average length of an incubation bout (two dimensions – survey and year). We analyzed the latter to distinguish between groups that have uninterrupted incubation periods and those that may spend a similar amount of time incubating but are on and off the nest numerous times. Total incubation length and mean incubation length were our dependent variables, respectively. Treatment, time of day, and group size were our independent variables, and year was included in the model as a random blocking factor. We included time of day in our model because it is unknown whether incubation behavior varies by this measure. We classified time of day as 'morning' (until 1000 hours), 'noon' (1001 – 1400 hours), or 'afternoon' (after 1400 hours). We included group size because helpers are known to assist with incubation (Khan et al. 2001, Walters 1990); thus, larger groups may have shorter mean incubation bouts.

We used doubly repeated measures analysis of covariance to analyze provisioning surveys, with total number of visits as our dependent variable (survey and year). Treatment, group size, brood size, age of nestlings, and time of day were our independent variables. Year was included in the model as a random blocking factor. We included group size in our model to ensure that the number of adults in a group did not influence the total number of nest visits. We included brood size in our model because nests with more nestlings likely receive more visits. We defined brood size as the number of nestlings present at the time of banding.

We performed all analyses with SAS (SAS 9.1.3, 2002 – 2003). We used PROC CORR for correlation analyses, PROC GENMOD for all logistic regression analyses, and PROC MIXED for all other analyses. For repeated measures analyses, we modeled the covariance structure as compound symmetry (exchangeable), which assumes constant variance for each measurement and constant covariance between any two measurements. We considered results significant at $p = 0.05$, with p-values < 0.10 considered marginally significant. We retained only significant or marginally significant interactions in our models. Our null hypothesis was that military training activity (i.e., treatment) would not affect any aspect of red-cockaded woodpecker behavior or demography. We present means ± standard errors in parentheses.

RESULTS

Demographic Measures

We did not include any covariates (group size, male breeder age, female breeder age) in our model of male breeder turnover because all were non-significant for all groups (all clusters pooled together, control and experimental clusters pooled together, and reference, control, and experimental clusters separately). We did not include any covariates in our model of female breeder turnover either, because none were significant for more than one group. Given their greater number (n = 45), more variable group size, and older breeders, pre-existing reference clusters provided a more accurate measure of correlations of group size, male breeder age, and female breeder age with demographic measures. Therefore, when correlation analyses differed on which covariate provided the strongest significant correlation with clutch size and fledglings per potential breeding group, we included in our models the covariate that had the strongest relationship for reference clusters (female breeder age and group size, respectively). Four of our models included the covariate that had the strongest relationship with our respective measures for four of the five groups: nesting effort (female breeder age), fledglings per successful nest (group size), female mortality (female age), and male mortality (male age). For our nest failure model we included male breeder age, which was significant for control clusters and control and experimental clusters combined. For our partial brood loss model we included group size, which was significant for reference clusters and all clusters combined.

Military training activity restrictions did not significantly affect recruitment cluster occupation within two years of availability (n = 18, χ^2 = 0.27, df = 1, p = 0.60), cluster occupation in general (n = 162, χ^2 = 0.48, df = 1, p = 0.49), or cluster occupation by a potential breeding group (n = 134, χ^2 = 0.02, df = 1, p = 0.90). Six of nine control recruitment clusters were occupied within two years of availability; 80% of all control clusters were occupied (n = 83 cluster-years). Birds occupied seven of nine experimental recruitment clusters within two years of availability and 86% of all experimental clusters (n = 81 cluster-years). Clusters containing potential breeding groups accounted for 88% of all occupied control clusters (n = 66 cluster-years) and 86% of all occupied experimental clusters (n = 70 cluster-years). Year did not influence cluster occupation (χ^2 = 7.04, df = 4, p = 0.13) or cluster occupation by a potential breeding group (χ^2 = 4.57, df = 4, p = 0.33).

Military training activity restrictions did not significantly impact nesting effort (n = 114, χ^2 = 0.15, df = 1, p = 0.70) or nest failure (n = 97, χ^2 = 0.00, df = 1, p = 0.95). Eighty-six percent of potential breeding groups in control clusters nested (n = 58 group-years) while 82% of groups in experimental clusters nested (n = 60 group-years). Eighteen percent of control nests failed (n = 50) whereas 20% of experimental nests failed (n = 49). Both year (χ^2 = 12.22, df = 4, p = 0.03) and female breeder age (χ^2 = 8.70, df = 1, p = 0.003) significantly affected whether a group nested, with young females being less likely to nest. Year (χ^2 = 1.98, df = 4, p = 0.74) did not influence nest failure; however, male breeder age had a marginally significant negative relationship with nest failure (χ^2 = 3.82, df = 1, p = 0.05).

Although mean clutch size was greater in control nests than experimental nests (3.28 ± 0.12 control, 3.10 ± 0.13 experimental), the difference was not statistically significant (n = 95, $F_{1,26.7}$ = 0.22, p = 0.64). However, military training activity restrictions significantly impacted partial brood loss (n = 78, $F_{1,20.4}$ = 5.00, p = 0.04). Control nests suffered higher partial brood loss compared to experimental nests (n = 41, 0.46 ± 0.03 control; n = 39, 0.35 ± 0.04 experimental); however, this result was not consistent among years (Fig. 2). Clutch size did not vary among years ($F_{4,70.8}$ = 1.04, p = 0.39) or with female breeder age ($F_{1,74.9}$ = 0.16, p = 0.69). Neither year ($F_{4,62.1}$ = 0.88, p = 0.48) nor group size (n = 78, $F_{1,26.1}$ = 0.35, p = 0.56) significantly influenced partial brood loss.

Military training activity restrictions did not affect the number of fledglings produced per successful nest (1.80 ± 0.09 control, 1.92 ± 0.12 experimental; n = 78, $F_{1,22.4}$ = 0.48, p = 0.49) or the number of fledglings produced per potential breeding group (1.28 ± 0.13 control, 1.25 ± 0.14 experimental; n = 116 group-years, $F_{1,62.2}$ = 2.47, p = 0.12). Both year and group size significantly influenced both number of fledglings produced per successful nest ($F_{4,52.3}$ = 2.81, p = 0.03; $F_{1,55.7}$ = 6.86, p = 0.01) and number of fledglings produced per potential breeding group ($F_{4,90.6}$ = 2.68, p = 0.04; $F_{1,68.4}$ = 6.66, p = 0.01). A year by group size interaction was marginally significant for fledglings produced per successful nest ($F_{4,50.9}$ = 2.08, p = 0.10), whereas a treatment by group size interaction was marginally significant for fledglings produced per potential breeding group ($F_{1,65.8}$ = 2.95, p = 0.09).

Neither military training activity restrictions nor year significantly impacted female breeder turnover (n = 72 bird-years; treatment, χ^2 = 0.36, df = 1, p = 0.55; year, χ^2 = 1.93, df = 3, p = 0.59). Nine percent (n = 36 bird-years) of breeding females in control clusters moved

between breeding seasons while 14% of females in experimental clusters moved (n = 36 bird-years). Male breeder turnover was less frequent than female breeder turnover (0% control, n = 32 bird-years; 2.9% experimental, n = 34 bird-years). However, our model for male breeder turnover failed to converge because no males in control clusters moved and only 1 male in experimental clusters moved.

Neither military training activity restrictions nor year affected female (n = 161 bird-years; $\chi^2 = 0.10$, df = 1, p = 0.76; $\chi^2 = 3.44$, df = 3, p = 0.33) or male mortality (n = 210 bird-years; $\chi^2 = 0.09$, df = 1, p = 0.76; $\chi^2 = 3.06$, df = 3, p = 0.38), when all status classes were considered together. Thirty-four percent of females in control clusters (n = 79 bird-years) and 33% of females in experimental clusters (n = 82 bird-years) perished, while 33% of males in control clusters (n = 99 bird-years) and 32% of males in experimental clusters (n = 111 bird-years) died. Female age had a highly significant effect on female mortality ($\chi^2 = 11.05$, df = 1, p = 0.0009), while male age had a marginally significant effect on male mortality ($\chi^2 = 3.78$, df = 1, p = 0.052), with both younger and older birds having higher mortality rates in both sexes. Training activity restrictions did not influence mortality rates for breeding males and females, fledgling males and females, or male helpers; results are not reported here. Small sample sizes precluded comparison of mortality between treatments for solitary males, helper females, and floater males and females.

Behavioral Measures

Roost times did not differ between treatments (n = 305, $F_{1,297} = 0.69$, p = 0.41). Individuals in control clusters roosted 29.6 ± 0.70 minutes before sunset; birds in experimental clusters roosted 31.1 ± 0.74 minutes before sunset. However, month significantly altered roost time ($F_{6,297} = 4.48$, p = 0.0002; Fig. 3).

Treatment did not significantly affect total incubation amount ($F_{1,87.9} = 2.43$, p = 0.12); however, it did impact incubation bout length ($F_{1,105} = 4.42$, p = 0.04; Fig. 4). We conducted 133 incubation surveys (68 control, 65 experimental), during which control groups incubated 52.5 ± 1.1 minutes per hour, with incubation bouts lasting 25.0 ± 1.8 minutes, whereas experimental groups incubated 49.7 ± 1.2 minutes per hour, with incubation bouts of 22.6 ± 1.7 minutes. Total incubation length did not vary by time of day ($F_{2,111} = 1.50$, p = 0.23) or group size ($F_{1,83.1} = 0.62$, p = 0.43); however, time of day ($F_{2,118} = 4.91$, p = 0.009) significantly affected incubation bout length. While group size had no influence on mean incubation length ($F_{1,100} =$

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2.53, p = 0.11), there was a marginally significant group size by treatment interaction ($F_{1,106}$ = 3.60, p = 0.06; Fig. 5).

Total feeding visits per hour did not differ by treatment (10.7 ± 0.54 control, n = 143; 9.1 ± 0.47 experimental, n = 130; $F_{1,63.8}$ = 1.66, p = 0.20). Both brood size ($F_{1,66.2}$ = 20.66, p <.0001) and nestling age ($F_{1,70.2}$ = 12.75, p = 0.0006) significantly influenced the number of feeding visits, while a time of day effect was marginally significant ($F_{1,205}$ = 3.17, p = 0.06). Group size did not influence provisioning rates, however, a significant group size by treatment interaction was present ($F_{1,63.3}$ = 4.53, p = 0.0372; Fig. 6). We used variance components to model our correlation structure (default in SAS PROC MIXED) for this analysis because using compound symmetry produced an infinite likelihood.

DISCUSSION

Demographic Measures

Failure to detect a significant effect of military training activity restrictions on occupation of clusters, occupation of clusters by a potential breeding group, and male and female breeder turnover is likely attributable to the high competition for high quality territories containing cavity trees observed in this species (Walters 1991, Walters et al. 1992). While female breeders moved more frequently than male breeders, the turnover rates we observed are comparable to those reported for the Sandhills population, located in south-central North Carolina (0% for males, 12% for females; Walters et al. 1988). It is not surprising, given the importance to nonbreeding adults of acquiring and maintaining a breeding position, that intermittent disturbance from military training activity would not dissuade them from doing so.

The mortality rates we observed are higher than both those reported for the Sandhills population (Walters et al. 1988, Walters 1990, Khan and Walters 2002) and observed on Camp Lejeune by Khan and Walters (2002) (Table 1). However, the latter study assessed effects of group size on breeder survival, and thus, only considered mortality rates for male and female breeders. The inclusion of fledglings and floaters in our calculations is the likely cause for the discrepancy between the two studies, as both classes exhibit decreased survival rates (Walters et al. 1988). The difference between mortality rates on Camp Lejeune and in the Sandhills could be linked to differences in habitat type. The Sandhills population inhabits an upland sandhills ecosystem with well-drained, nutrient-poor, sandy soils (for a more detailed description see

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Walters et al. 1988), whereas the Camp Lejeune population inhabits a wetter, more-poorly drained, pine flatwoods ecosystem. Differing climates could also cause variation in mortality rates between a coastal (Camp Lejeune) and an inland site (Sandhills).

The lack of a significant relationship between training activity restrictions and both nesting effort, nest failure, clutch size, and ultimately number of fledglings produced suggest red-cockaded woodpeckers may habituate to disturbance from military training. Our results are similar to Anderson et al. (1989), who reported no effect of helicopter overflights on red-tailed hawk (*Buteo jamaicensis*) nest success. Likewise, Palmer et al. (2003) determined that military jet disturbance did not significantly influence peregrine falcon (*Falco peregrinus*) nest failure or productivity, although disturbed nests tended to fail more often and produce fewer young.

Perplexing, however, is the higher partial brood loss we observed in control clusters. Yet control clusters did not consistently exhibit higher rates of brood loss across years, and it seems that data from 2002 are driving this result (Fig. 2). Indeed, analyzing partial brood loss with the same model as above (treatment, year, and group size as independent variables) but excluding data from 2002 resulted in no difference between treatments (n = 62, $F_{1,18.4}$ = 0.88, p = 0.36). Also, in 2002 it appears that control clusters did not exhibit higher partial brood loss as much as reference and experimental clusters experienced lower partial brood loss compared to other years. This aberration in 2002 could suggest a combination of habituation to and impact from military training activity. Recall that reference clusters are like control clusters because both are marked as restricted. In 2002, with many troops overseas, disturbance from military training activity could have been substantially diminished. Birds in experimental clusters could have habituated to increased military training activity in 2000 and 2001, while birds in reference clusters could have habituated to less frequent disturbance over a period of years, such that when the stimulus was reduced, nests in both reference and experimental clusters exhibited lower rates of partial brood loss. Perhaps birds in control clusters were not accustomed to even infrequent disturbance, and thus responded more strongly whenever disturbance from military training activity did occur. However, that no difference was found among treatments when 2002 was excluded suggests that habituation is not protecting experimental clusters under more typical training regimes.

Behavioral Measures

More frequent disturbance from military training activity could have caused incubating birds in experimental clusters to flush from their nests, resulting in shorter mean incubation bout lengths than control clusters. However, this shorter incubation bout length did not translate into any effect at the demographic level, likely because experimental clusters compensated by incubating a total amount of time similar to control clusters. While we found no effect of group size on mean incubation bout length, Khan and Walters (2002) determined that incubation bouts are divided equally among group members. The pattern we observed in control clusters suggests that individual incubation bouts are shorter in larger groups (Fig. 5). However, a marginally significant group size by treatment interaction was present in our model, possibly precluding a significant effect of group size on mean incubation length. Additionally, while control clusters exhibited a linear decrease in mean bout length with increasing group size, incubation bout lengths were similar across all observed group sizes in experimental clusters (Fig. 5).

Feeding rates in control and experimental clusters were similar to those reported for clusters in longleaf pine habitat in Louisiana (Conner et al. 1999) and eastern Texas (Schaefer et al. 2004). Nestling provisioning rates in the Sandhills, Camp Lejeune, and Croatan National Forest combined (all in North Carolina) were lower and more variable; however, sample size was limited (Khan and Walters 2002). On Fort Benning (Georgia), feeding rates of clusters in loblolly pine habitat did not vary by proximity (adjacent or distant) to small arms and artillery ranges (Doresky et al. 2001).

Our analysis of provisioning rates revealed a significant group size by treatment interaction. Control clusters exhibited a linear, slightly elevated rate of feeding with increasing group size (Fig. 6), consistent with a report of higher feeding rates (but not significantly) of nests with a helper (Khan and Walters 2002). Experimental clusters show an inconsistent effect of group size on feeding rates. That the same pattern appears in both mean incubation length and total feeding visits (consistent for control, inconsistent for experimental), coupled with significantly shorter mean incubation bouts in experimental clusters, suggests that behavioral disturbance from military training activities was more frequent in experimental clusters.

Overall Assessment

Overall, we found little evidence that removing restrictions on military training activities impacted red-cockaded woodpecker behavior, and where effects on behavior did occur, they did

not result in impacts on demography. Besides treatment by group size interactions in our mean incubation length and total feeding visits models, the only measures that differed between experimental and control clusters were partial brood loss and mean incubation bout length, which only revealed a contradictory effect of training activity on partial brood loss (higher for control clusters) and mean incubation length (lower for experimental clusters). Thirteen of 15 behavioral and demographic measures did not differ between treatments. Habituation is one explanation for the lack of differences we observed and the higher partial brood loss observed in control clusters. Another possibility is that the 200ft (61m) buffer zone surrounding clusters on Camp Lejeune is insufficient to protect red-cockaded woodpeckers from disturbance. Alternatively, it may be that troops did not adjust their activity in accordance with buffer markings, failing to refrain from restricted activities within marked buffers, being reluctant to engage in training activities in unmarked clusters, or both. In all of these cases the birds would not perceive a difference between treatments.

Distance to disturbance has been reported as a consistent predictor of response in several avian studies (Grubb and Bowerman 1997, Stalmaster and Kaiser 1997, Trimper et al. 1998, Delaney et al. 1999, Ward et al. 1999). Breeding bald eagles (*Haliaeetus leucocephalus*) responded less frequently with increased distance to aircraft, but reacted (alert behavior or flushing) more often and more severely as the nesting season progressed and nest attendance requirements declined (Grubb and Bowerman 1997). Grubb and Bowerman (1997) concluded that increasing the buffer area around breeding bald eagles from 400m to 600m would decrease response rates from 32% to 19%. Wintering bald eagles flushed less with greater distance to military weapons firing events, helicopter overflights, and boats; however, those flushed from feeding or perching on the ground only resumed these activities after an extended period of time (Stalmaster and Kaiser 1997). Stalmaster and Kaiser (1997) recommended a general buffer zone of 300-500m and exclusion of aircraft below 300m to reduce flushing rates. Mexican spotted owls increased flush frequency with decreased distance to helicopter and chainsaw disturbance (Delaney et al. 1999). Delaney et al. (1999) suggested a 105m buffer area around nests because owls did not flush when stimuli > 105m. Lastly, the Federal Aviation Administration suggests an altitude > 600m for sensitive wildlife areas (reported in Ward et al. 1999). While species sensitivity to disturbance undoubtedly varies greatly, a considerable discrepancy exists between the 200ft red-cockaded woodpecker buffer and the afore-mentioned distances, most of which are

an order of magnitude greater. Thus, it may be that red-cockaded woodpeckers did not perceive disturbance as being different in marked and unmarked clusters.

Several studies suggest that naïve birds react more strongly to disturbance. Wintering bald eagle sub-adults flushed more often than adults in response to disturbances (Stalmaster and Kaiser 1997). Anderson et al. (1989) reported stronger avoidance behavior (crouch/remain motionless, flight intention, flushed, evasive flight) by nesting red-tailed hawks in an area where helicopter overflights were allowed only 1 year prior to study initiation, compared to birds in an area exposed to extensive helicopter activity for roughly 25 years. They also reported no effect of helicopter disturbance on nest success and suggested that nesting red-tailed hawks appear to habituate, though observations suggested that naïve birds might react to disturbance prior to habituation. Red-cockaded woodpeckers in experimental clusters may have experienced more disturbances but habituated to military training activity. In turn, birds in control clusters may have been more sensitive when disturbances did occur, leading to our inconsistent results.

Finally, we were unable to determine whether military training truly differed between control and experimental clusters. While clusters were marked by the presence (control) or absence (experimental) of a white-painted buffer, all cavity trees were marked with a blue-painted double-band to facilitate location for monitoring and fire protection purposes. It is possible that soldiers cued in on marked cavity trees, rather than the buffer zone, and avoided clusters regardless of whether they were restricted.

MANAGEMENT RECOMMENDATIONS

Many of the patterns that emerged from our analyses concerning group size and breeder age on demographic measures are consistent with those reported in the well-established body of red-cockaded woodpecker literature. If training activity impacts demography, it appears the effects are subtle and mostly overwhelmed by these demographic patterns. Thus, we believe our models provide a fair test of military training activity restrictions.

Even so, while we found no consistent significant effect of military training at the population level, we feel that removing restrictions entirely would be premature. There are some indicators of impacts of removing restrictions on behavior in the variable effect of group size on both mean incubation length and nestling provisioning rates observed. We recommend another study to more accurately assess military training activity effects, by marking entire areas as

experimental, such as high-use training areas, and restricted, low-use control areas, to ensure that training activity truly differs between treatments. This study design might yield more accurate results of whether training activity affects red-cockaded woodpecker behavior and, more importantly, demography at the population level. If possible, quantifying the amount of training activity would allow confident interpretation of results from a future study.

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Table 1.1. Comparison of mortality rates in two populations of red-cockaded woodpeckers, separated by sex and status class. Both populations are located in North Carolina, USA. Shaded cells represent sample sizes of <10 for one or more groups within our study (control, experimental, reference).

Status	Female		Male	
	Sandhills	**Camp Lejeune**	**Sandhills**	**Camp Lejeune**
Breeder	31-32[a,b]	11.9-27.0[c]	24[a,b]	15.2-24.4[c]
	30[d]	21.9[d]	23.6[d]	17.4[d]
Fledgling	66-68[a,b]	57.1-61.8[c]	56-57[a,b]	46.0-59.3[c]
Helper		34.6-50.0[c]	20-22[a,b]	16.9-20.0[c]
Floater	45[b]	24.4-40.0[c]	38[b]	0.0-66.7[c]
Solitary			38[a,b]	33.3-100[c]

[a] Data are from Walters et al. 1988
[b] Data are from Walters 1990
[c] Data are from this study; ranges encompass control, experimental, and reference clusters
[d] Data are from Khan and Walters 2002

Fig. 1.1. Map of Marine Corps Base Camp Lejeune, North Carolina, showing major training areas. Black polygons portray red-cockaded woodpecker clusters with buffer zones 2001-2005.
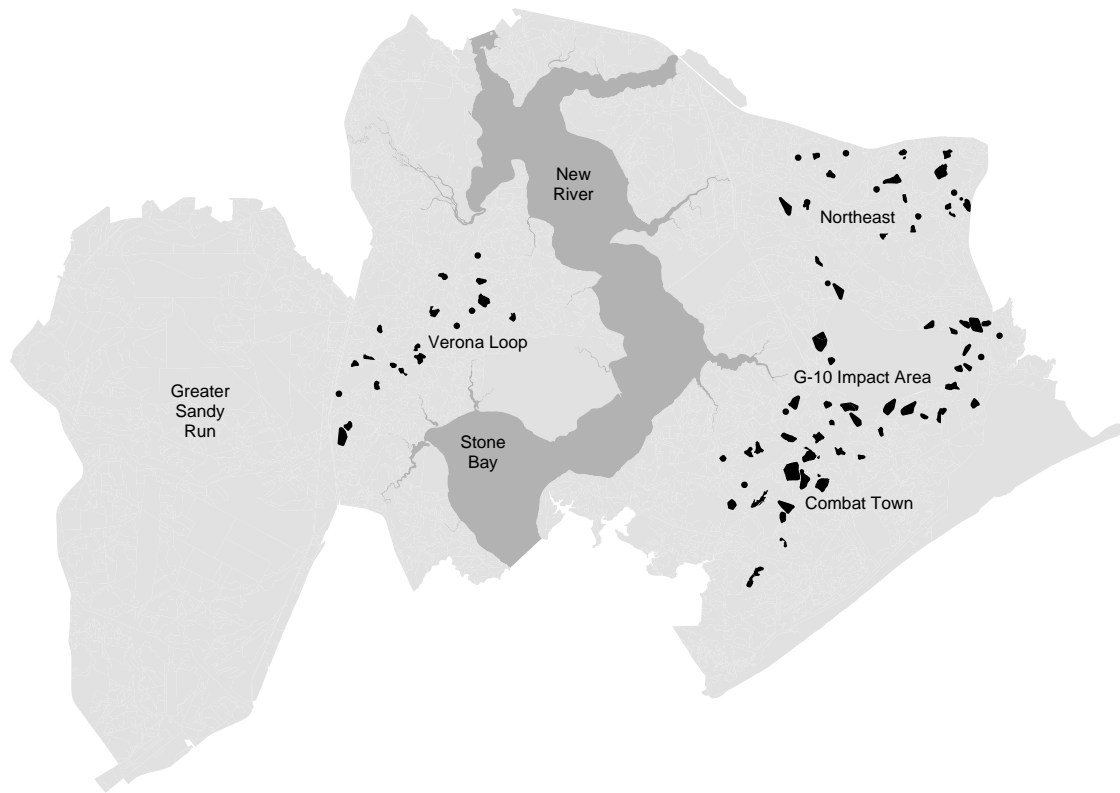
Fig. 1.2. Comparison of red-cockaded woodpecker partial brood loss (mean ± SD) for reference, control, and experimental clusters on Marine Corps Base Camp Lejeune, NC, 2001-2005. Sample sizes are indicated above the bars.
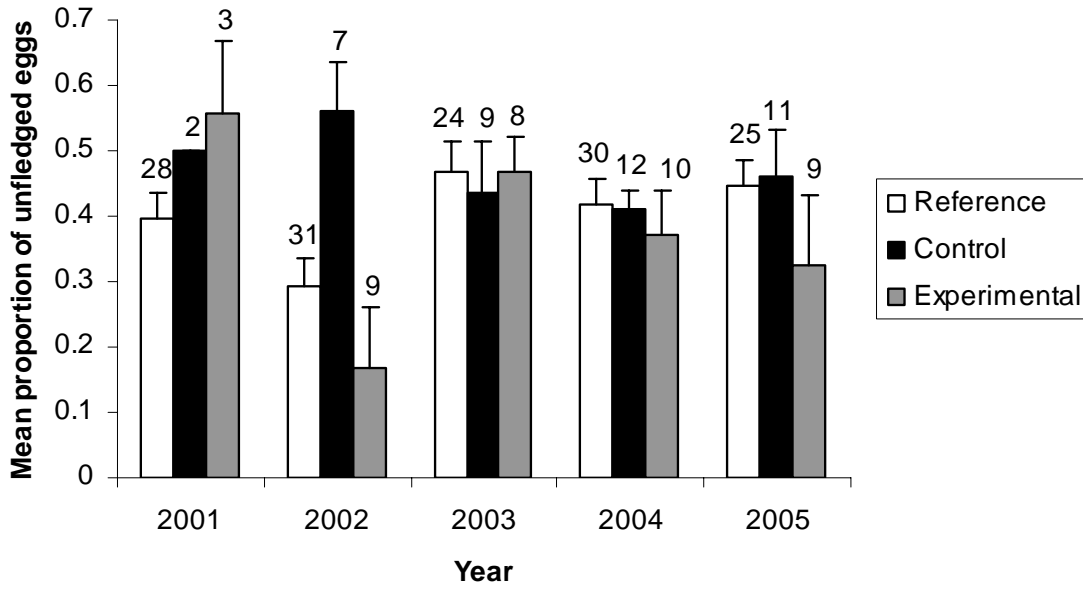
Fig. 1.3. Comparison of red-cockaded woodpecker roost time (mean ± SE) for control and experimental clusters on Marine Corps Base Camp Lejeune, NC, 2001-2005. Sample sizes are indicated above the bars.
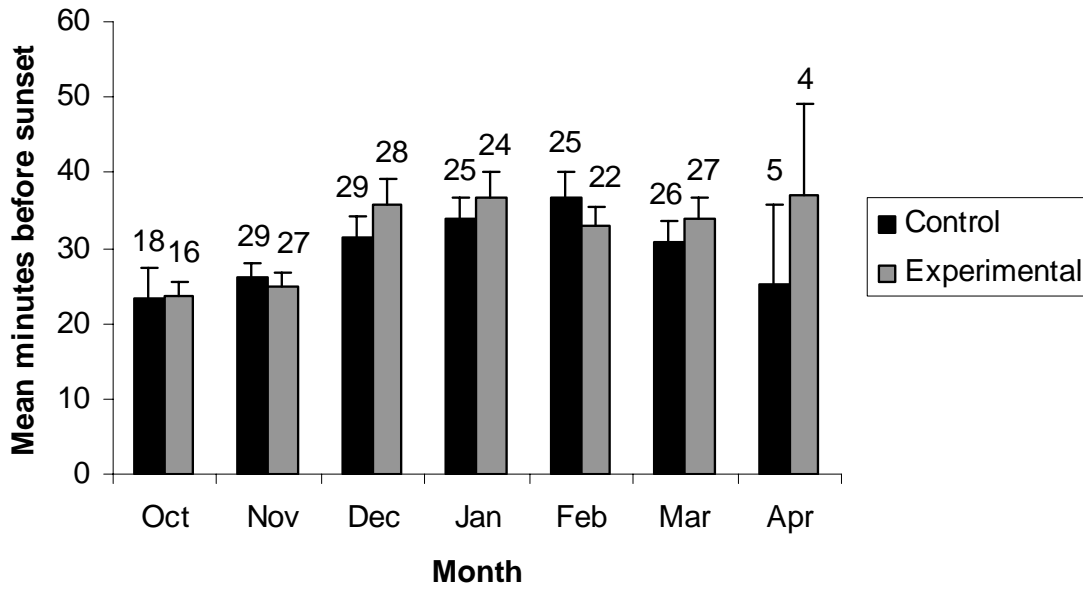
Fig.1.4. Comparison of red-cockaded woodpecker incubation bout length (mean ± SE) for control and experimental clusters on Marine Corps Base Camp Lejeune, NC, 2001-2005. Sample sizes are indicated above the bars.
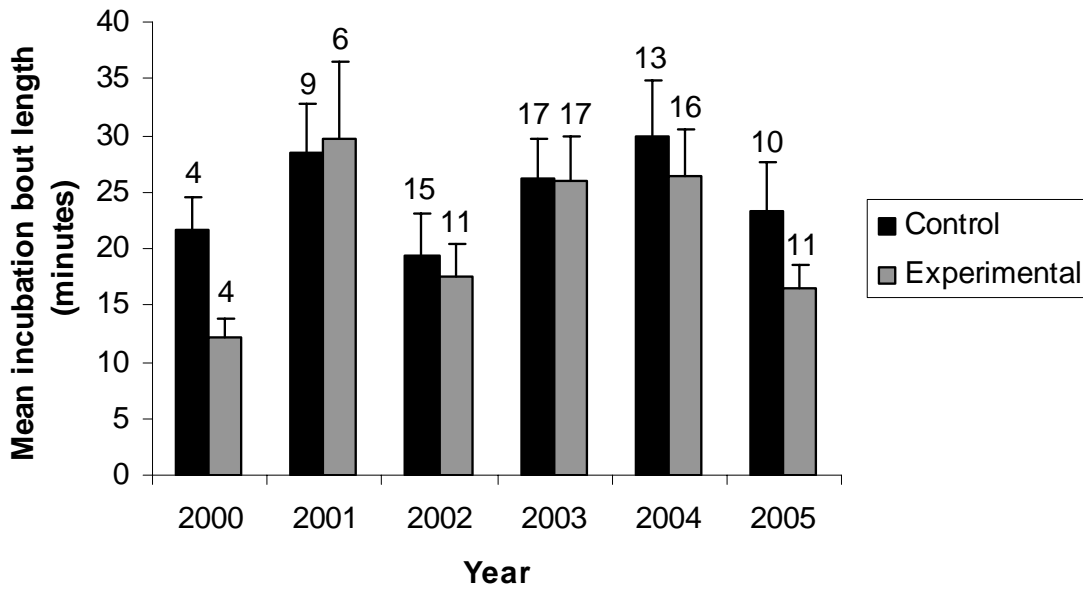
Fig. 1.5. Comparison of red-cockaded woodpecker incubation bout length (mean ± SE) by group size for control and experimental clusters on Marine Corps Base Camp Lejeune, NC, 2001-2005. Sample sizes are indicated adjacent to each point; where means are too close to distinguish visually, control sample size is listed first.

Fig. 1.6. Comparison of red-cockaded woodpecker provisioning rate per nest (mean ± SE) by group size for control and experimental clusters on Marine Corps Base Camp Lejeune, NC, 2001-2005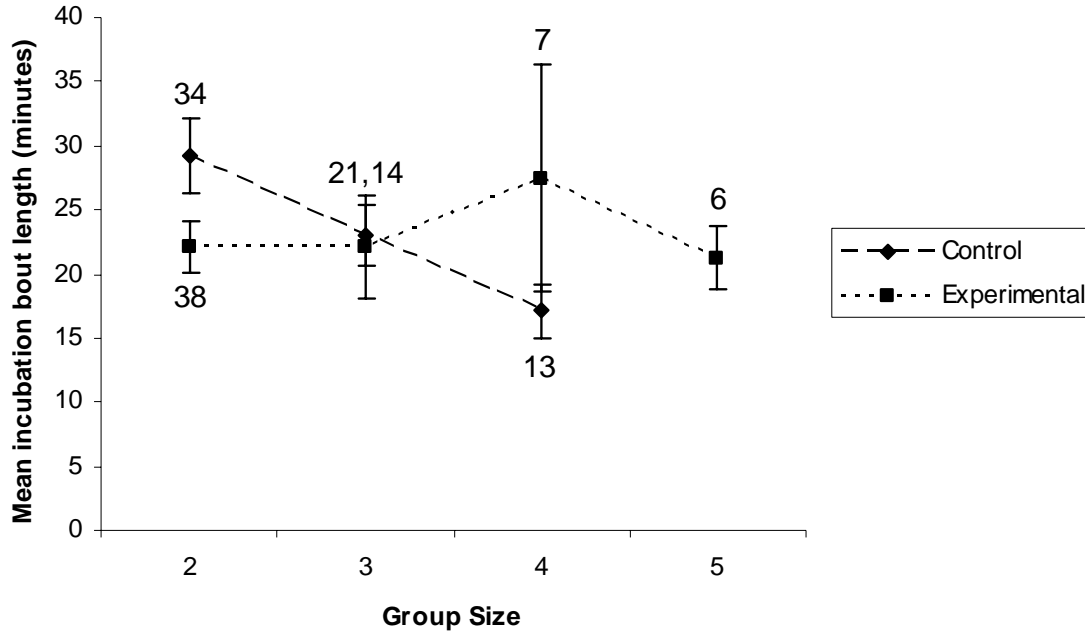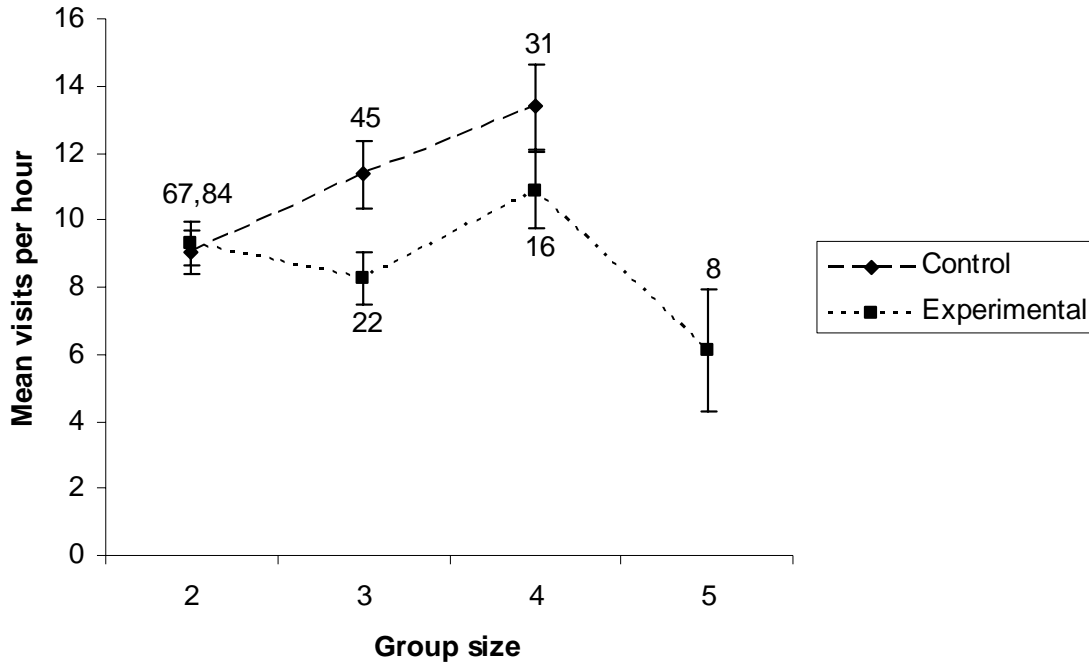. Sample sizes are indicated adjacent to each point; where means are too close to distinguish visually, control sample size is listed first.

CHAPTER 2: NEW TERRITORY FORMATION IN THE COOPERATIVELY BREEDING RED-COCKADED WOODPECKER

ABSTRACT

In species exhibiting cooperative breeding behavior, emphasis is placed on constraints on acquiring a suitable breeding position and queuing in the form of helping or floating to obtain a breeding vacancy. However, despite this driving force that underlies cooperative breeding social systems, few studies have described territory creation events and factors that induce new territory formation. I used 20 years of demographic data collected as part of a long-term monitoring study of Red-cockaded woodpeckers (*Picoides borealis*) to investigate mechanisms that stimulate territory creation in this cooperatively breeding species. Because the Red-cockaded woodpecker is an endangered species, I sought to determine how to naturally increase populations, as well as contribute greater understanding to cooperative breeding systems. I determined that young male helpers and affiliated floaters bud, while young male unaffiliated floaters and solitary males pioneer. Intensified competition, measured as an increased proportion of nonbreeding males in the population, was positively associated with new territory formation. This study also revealed the large role that floaters play in territory creation events in this system.

INTRODUCTION

Cooperative breeding systems have stimulated much research regarding demographics of individual species, the evolutionary basis of helping behavior, and the causes underlying the evolution of this social system. Theories about the latter such as ecological constraints and benefits of philopatry (Emlen 1984; Stacey and Ligon 1987, 1991) focus on limitations to acquiring suitable breeding positions. A characteristic of the most common types of cooperative breeding systems is the predominance of turnover on existing territories, as opposed to creation of new territories, in acquiring breeding positions, but new territory formation does occur. Given the emphasis placed on attainment of breeding positions as a driver in the evolution of this social system, it is surprising that few studies mention the creation of new territories, and even fewer have investigated mechanisms promoting territory creation activities such as budding and

pioneering (but see Woolfenden and Fitzpatrick 1978, 1990; and Komdeur and Edelaar 2001*ab*) that are alternatives to helping. Territorial budding (*sensu* Woolfenden and Fitzpatrick 1978) divides one territory into two, while pioneering creates a new territory in formerly unoccupied habitat. Pioneering may not be an option in species constrained by absolute habitat saturation, but budding may be widespread and understudied among cooperative breeders. My objective was to investigate factors that trigger budding and pioneering in the Red-cockaded woodpecker (*Picoides borealis*).

The Red-cockaded woodpecker is a federally endangered species, endemic to open, mature pine forests of the southeastern United States. It is unique among North American cavity nesters because it constructs roost and nest cavities in live pine trees (USFWS 2003). Cavity excavation may take several years due to the difficulty of construction in live pines (Jackson et al. 1979; Harding and Walters 2002, 2004), which has caused cavities to be a critical resource that appears to have promoted the evolution of cooperative breeding in this species (Walters et al. 1992). Rather than construct cavities in unoccupied habitat, Red-cockaded woodpeckers compete intensely for territories with existing cavities (Walters 1991, Walters et al. 1992), with the natural creation of new territories being rare (Hooper 1983, Walters 1990).

Red-cockaded woodpecker groups typically contain a breeding pair and 0-4 nonbreeding helpers, usually male offspring from prior breeding attempts (Lennartz et al. 1987, Walters et al. 1988, Walters 1990). Helpers assist in incubation and provisioning nestlings and fledglings, as well as territory defense. However, helpers do not engage in extra-pair copulations even if the opposite sex breeder is unrelated, and thus gain fitness benefits from helping mostly indirectly through assisting kin (Haig et al. 1994, Khan and Walters 2000). Male helpers inherit the natal territory upon death of the breeding male and will pair with the widowed female if she is unrelated to him. If she is a relative, the female leaves and the male attracts a new female. Helpers may also disperse short distances to fill vacancies on nearby territories.

Red-cockaded woodpecker population size, as measured by the number of groups, is not greatly affected by natality or mortality because male helpers act as a buffer between these processes and number of breeders (Walters et al. 2002b, USFWS 2003). Individuals rapidly occupy breeding vacancies when mortality outweighs reproduction, while helper class numbers grow when births exceed deaths (Walters 1991, Heppell et al. 1994). Thus, the number of breeding pairs varies little across years. Conversely, because cavities are a limiting resource and

an essential component of high quality territories, cavity tree dynamics have a substantial impact on population demography (Walters et al. 1992). Therefore, population dynamics are driven primarily by the availability of suitable territories – i.e. habitat containing cavity trees.

While rare, territory creation occurs naturally through budding and pioneering in Red-cockaded woodpeckers (Hooper 1983). Budding involves splitting one territory and its associated cavity trees and generally occurs more frequently than pioneering (Hooper 1983, Walters 1991, Conner et al. 2001). Pioneering requires excavating new cavities in formerly unoccupied habitat (Hooper 1983, Walters 1991, Conner et al. 2001). Budding is a relatively safe option due to the presence of completed cavities, whereas pioneering is risky because an individual will have to roost in the open until a cavity is completed. Budding and pioneering rates vary among populations as to which process predominates and to what extent, but generally produce population growth rates of no more than 1-2% combined annually (Conner et al. 2001). Because territory creation rates are so low range-wide, they limit the potential for recovery. An exceedingly lengthy time period would be required to recover the species if left solely to expand on its own through budding and pioneering (USFWS 2003).

Artificial cavity construction has been employed since 1989 to stabilize declining populations and stimulate population growth (Conner et al. 2001). Cavity provisioning involves the creation of artificial cavities in live pines by applying a drilling technique (Copeyon 1990) or by inserting preformed boxes (Allen 1991). Both techniques address the lengthy process of natural cavity construction and the rarity with which new territories are created. Artificial cavities installed in previously unoccupied suitable habitat are termed recruitment clusters and are readily occupied, leading to new group formation (Walters et al. 1992).

Management costs for both translocation and artificial cavity construction are high and prohibitive long-term. There is also an opportunity cost of money and time that could be spent on other conservation activities and species. Thus, it is important to determine what induces budding and pioneering in order to enable Red-cockaded woodpecker populations to grow more rapidly through natural processes. Additionally, spatially explicit individual-based population modeling for Red-cockaded woodpeckers could be improved by more accurate input of budding and pioneering parameters (Scheigg et al. 2005). Currently, no one has examined the causes underlying these processes. Marine Corps Base Camp Lejeune exhibits the highest rates of budding and pioneering recorded (Walters 2004), and therefore provided a unique opportunity to

determine what factors promote natural territory creation. In this paper, I examine these processes and relate my findings to the conservation of Red-cockaded woodpeckers and the evolution of cooperative breeding systems.

METHODS

Study Area

Marine Corps Base Camp Lejeune is located in Onslow County along the central coast of North Carolina. The Main Base is comprised of 61,110 ha, 10,522 of which is open water (Convery 2002). Most of the Red-cockaded woodpecker groups are associated with longleaf pine (*Pinus palustris*), however some are found in loblolly (*P. taeda*) and pond pine (*P. serotina*) (Zwicker and Walters 1999). For a more detailed description, including habitat types and frequency see Zwicker and Walters (1999).

All Red-cockaded woodpecker groups occur on the Main Base (Fig. 1). The Greater Sandy Run Area of 16,593 ha was purchased in 1992 and is adjacent to and southwest of the Main Base; it contains no Red-cockaded woodpecker groups. The eastern portion of the Main Base is effectively separated from the western portion by Stone Bay and the New River (Fig. 1). Most Red-cockaded woodpecker groups are found in the Combat Town and Northeast training areas and the G-10 impact area, located in the eastern portion. The Verona Loop Training Area houses a smaller subpopulation located in the western portion. Dispersal between the Combat Town training area, G-10 impact area, and Northeast training area is frequent, whereas dispersal between the eastern and western subpopulations is rare.

Data Collection

I used 20 years of breeding season monitoring data collected as part of a long-term study on Camp Lejeune (see Walters et al. [1988] for a detailed description of breeding season monitoring). Briefly, clusters were monitored every 7-9 days to check for the presence of a nest. Once a nest was detected, it was examined by either climbing with Swedish ladders and using a drop light and mirror or with a camera mounted on a telescoping pole. Once nestlings reached days 5-10, they were pulled from the cavity using a monofilament noose and banded with a uniquely numbered aluminum leg band from the U.S. Fish and Wildlife Service. Nestlings were also banded with a unique color leg band combination to facilitate individual recognition without recapture. Fledging checks were scheduled approximately 30 days post-hatch to verify whether

a nestling succeeded in fledging and to determine sex based on presence (male) or absence (female) of a red crown patch. A complete adult census was conducted each breeding season to determine which individuals were affiliated with each group in the population.

Predictions

I sought to determine what factors trigger budding and pioneering events and promote the prevalence of one over the other. I hypothesized that both social and ecological components influence territory creation rates. Because females have never been observed to bud or pioneer on Camp Lejeune, I restricted my analyses to males and investigated the relationship between male status, age, and helper dominance rank and initiation of territory creation events. Budding is often accomplished by a helper, but may also be achieved by an immigrant male (Conner et al. 2001). I expected helpers to accomplish most budding events and floaters and dispersing fledglings to perform most pioneering events. Floaters are individuals generally not associated with a particular group or territory. I did not expect breeders or solitary males to bud or pioneer because they already hold a breeding position (solitary males defend a territory but lack a mate). I predicted younger males would bud and pioneer because I assumed older males are better able to compete for breeding vacancies. Dominance rank relates to age because younger helpers are subordinate to older helpers. A dominant helper may be unlikely to bud considering it is next in line to obtain a breeding vacancy; if it inherits the natal territory, it will likely acquire a larger and presumably better territory than if it split off a piece of the territory by budding. Additionally, subordinates suffer a greater opportunity cost arising from an additional waiting period and foregone direct reproduction. Therefore, I expected lower ranking helpers to bud more often than dominants.

Conner et al. (2001) suggest the presence of large numbers of helpers or floaters promotes budding and pioneering by acting as a cue for nesting habitat saturation. Fewer vacancies available per competitor results in intensified competition. I predicted escalated competition would elevate budding and pioneering rates due to an increased reproductive cost of waiting for a breeding vacancy.

The distribution of available females may also affect territory creation events. A male may be unlikely to commit the costly act of budding or pioneering if there are few females available to pair with him. I expected more available females in the population to increase the number of budding and pioneering events.

USFWS (2003) hypothesized that differences in management, specifically the amount of prescribed burning and resultant habitat improvement, is one explanation for the variance in territory creation rates among populations. I predicted that if natal and surrounding habitat quality was high, a male would wait for a breeding vacancy or bud, whereas if it was low an individual would be more likely to disperse and pioneer. I also expected habitat quality of the pioneered territory to be higher than that of the natal territory.

Data Analyses

Because I was limited by a small sample size of only 25 buds and pioneers combined, I mostly restricted my analyses to univariate tests. I analyzed the relationship of territory creation events to status, age, and helper dominance rank using Fisher's Exact test. For the analysis of status, I used five male status classes: fledglings, helpers, breeders, solitary males, and floaters. I separated all males into four age classes: fledglings (HY, hatch-year, 0 years), 1-3 years (SY-4Y, second-year to fourth-year), 4-7 years (5Y-8Y), and 8 years and older (9Y+). I classified male ages in this way because these classes represent distinct stages in a male's life. Roughly half of male fledglings remain on their natal territory while the other half disperses (Walters et al. 1988). Males commonly help from ages 1-3, while most males have acquired a breeding vacancy by ages 4-7. Helpers age 8 or older are rare. I did not include unknown-aged birds in my analysis of association between age and territory creation events.

I assigned helpers a dominance rank within their group – 1,2,3, etc. – in accordance with decreasing age. Among nest mates, usually only the dominant male fledgling remains on the natal territory as a helper while subordinate male fledglings disperse (Pasinelli and Walters 2002). In the few cases where sibling males from the same nest remained on the natal territory as helpers in their second year, I assigned dominance to the individual that had the highest weight when banded as a nestling (see Pasinelli and Walters 2002).

I defined competition intensity as the ratio of the number of breeding vacancies to the number of competitors each year. I computed breeding vacancies as the number of breeding males that died plus the number of unoccupied suitable clusters available since the preceding breeding season. Unoccupied territories were considered suitable only if birds had inhabited them at some time during the past five years (Doerr et al. 1989). I counted any males that did not hold a breeding position – fledglings, helpers, and floaters – the previous breeding season as competitors. I also used the proportion of breeding positions vacant and the proportion of males

that were nonbreeders as additional measures of competition intensity. These three measures for the year preceding the bud or pioneer were used as independent variables and analyzed separately using simple linear regression to determine if an association existed between population-level competition intensity and the number of territory creation events. I used the proportion of males that were nonbreeders and proportion of breeding positions vacant rather than absolute numbers because there will always be more competitors and potentially more vacancies as a population increases. However, for the dependent variable I used the actual number of territory creation events because proportions do not constitute an adequate dependent variable for rare events: the proportion of males budding and pioneering each year ranged from only 0 to 0.04).

I considered female fledglings, helpers, and floaters as available. I tested for a relationship between the number of budding and pioneering events and the proportion of females available at the population level using simple linear regression.

I included group size in my territory quality model to separate effects of these two variables, because group size is often confounded with territory quality. Higher quality territories produce more offspring, which in cooperative breeders results in more young retained as helpers. Helpers in turn often increase reproductive success, further exaggerating the difference between low and high quality territories. I used the mean number of fledglings produced per potential breeding group (a territory containing at least one male and one female) as a measure of territory quality. I included only first nesting attempts in the analyses. I calculated this measure for the entire 20 years to obtain a population average, and also calculated this same measure for each individual territory. I defined the quality of an individual territory as the deviation from the population average. Higher quality territories will have a positive number reflecting more offspring produced. I divided this deviation by the number of adults in a group each year to obtain an individual's perception of territory quality (*sensu* Brouwer et al. *in press*). I analyzed the relationship between group size, territory quality, and the number of buds and pioneers using repeated measures logistic regression, with the number of buds and pioneers as the dependent variable and individual males as a repeated measure.

I performed all analyses with SAS (SAS 9.1.3, 2002 – 2003). I used PROC FREQ for Fisher's Exact tests, PROC GENMOD for all repeated measures logistic regression analyses, and PROC REG for all other regression analyses. For repeated measures analyses, I modeled the

covariance structure as compound symmetry (exchangeable), which assumes constant variance for each measurement and constant covariance between any two measurements. I considered results significant at p = 0.05. My null hypothesis was no relationship between territory creation events and any of the above measures.

RESULTS

Status was significantly associated with territory creation events, when both buds and pioneers were considered together (n = 2131 bird-years, p < 0.0001) and separately (buds: p < 0.001, pioneers: p < 0.0001) (Fig. 2). Breeders budded (2 events; 0.09% of breeder-years) and pioneered (1 event; 0.05%) less often than expected. Fledglings also budded (0 events) and pioneered (1 event, 0.05% of fledgling-years) less frequently than expected. Floaters both budded (4, 0.19%) and pioneered (7, 0.33%) more frequently than expected. Helpers budded (5, 0.23%) more often than expected, but the frequency with which helpers pioneered (4, 0.19%) equaled that expected. Solitary males pioneered (2, 0.09%) more often than expected, while the frequency with which they budded (0) equaled that expected.

Male age had a significant relationship with territory creation events, when both buds and pioneers were considered together (n = 1896 bird-years, p = 0.0003) and separately (buds: p = 0.0069, pioneers: p < 0.001) (Fig. 3). Young males budded (7 events, 0.37% of males ages 1-3) and pioneered (13, 0.69%) more frequently than expected. Middle-aged males pioneered less often than expected (1 event, 0.21% ages 4-7), but budded as often as expected (3, 0.16%). No older males (ages 8-17) budded or pioneered, which was expected given that older males comprise only 6.33% of the population.

Neither the ratio of the number of breeding vacancies to the number of competitors (n = 19; buds and pioneers combined, $r^2 = 0.11$, t = -1.46, p = 0.16, Fig. 4a; buds, $r^2 = 0.09$, t = -1.31, p = 0.21; pioneers, $r^2 = 0.11$, t = -1.45, p = 0.17) nor the proportion of breeding positions available (buds and pioneers combined, $r^2 = 0.03$, t = -0.69, p = 0.50, Fig. 4b; buds, $r^2 = 0.04$, t = -0.79, p = 0.44; pioneers $r^2 = 0.02$, t = -0.52, p = 0.61) had a significant relationship with territory creation events. However, the proportion of the population comprised of competitors was significantly and positively associated with budding and pioneering events (buds and pioneers combined, $r^2 = 0.29$, t = 2.63, p = 0.02, Fig. 4c; buds, $r^2 = 0.21$, t = 2.12, p = 0.05; pioneers, $r^2 = 0.32$, t = 2.80, p = 0.01).

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Male helper dominance rank did not have a significant relationship with territory creation events (n = 580 male helper-years, buds and pioneers together, p = 0.47; separate, buds: p = 0.21, pioneers: p = 0.17). The proportion of females available at the population-level was not significantly associated with the number of territory creation events, whether buds ($r^2 = 0.01$, t = 0.41, p = 0.69) and pioneers ($r^2 = 0.03$, t = 0.74, p = 0.47) were considered separately or together ($r^2 = 0.02$, t = 0.60, p = 0.55, n = 19; Fig. 4d). Neither territory quality per individual nor group size was significantly associated with budding and pioneering events when combined (n = 2293 bird-years; quality, $\chi^2 = 0.78$, df = 1, p = 0.38; group size, $\chi^2 = 0.55$, df = 1, p = 0.46) or considered separately (buds: quality, $\chi^2 = 0.64$, df = 1, p = 0.42; group size, $\chi^2 = 0.68$, df = 1, p = 0.41; pioneers: quality, $\chi^2 = 0.42$, df = 1, p = 0.51; group size, $\chi^2 = 0.00$, df = 1, p = 0.96).

DISCUSSION

My analyses revealed that young, male helpers and floaters bud, and young, male floaters and solitary males pioneer on Camp Lejeune, while breeders and fledglings rarely bud or pioneer. Increased competition for breeding vacancies also positively influences both processes. That neither the proportion of breeding positions nor females available at the population-level affected territory creation events is consistent with the argument that factors affecting an individual's decision will not be apparent or relevant at the population-level (Ridley et al. 2003, Brouwer et al. *in press*). Thus, the availability of breeding positions and females might have an impact at the local level, rather than the population level.

Floaters: an Underappreciated Strategy

That only 5 of 11 budding events were performed by helpers is not directly contrary to my predictions. Helpers did bud more often than expected by their frequency in the population. My error stems from assuming that helpers would perform most budding events, and not realizing the role of floaters in budding events. I suggest that floating is an under-appreciated strategy in this system that merits additional study.

Floaters can be classified into two categories – affiliated and unaffiliated – based on monitoring data (Walters et a. 1988; Walters 1990). Affiliated floaters are individuals that manage to become partly accepted by the resident birds; i.e. territorial conflicts are subdued and many affiliated floaters are allowed to forage somewhat peacefully. Unaffiliated floaters continue to search for breeding vacancies and range more widely over at least several territories.

While I did not include this distinction in my analyses, several points are interesting to note. Six of seven floaters that pioneered were unaffiliated, while three of four floaters that budded were affiliated. Thus, to clarify my original summary of which status classes bud and pioneer, affiliated floaters bud and unaffiliated floaters pioneer. Furthermore, while breeders budded less often than expected, I did not expect any breeders to bud or pioneer. However, the two breeders that budded were apparently forced out by floaters that had affiliated themselves with the group the year before the budding event. Rather than completely surrender their territories, these breeders defended a portion of their former territory and hence, budded. I suggest that floaters affiliate with a territory as a strategy for obtaining a breeding vacancy. Affiliated floaters benefit by familiarity with the territory (a benefit that has been cited for helpers, Emlen 1984), thereby perhaps being in a better position to evict the current breeder, or when they are unable, bud instead.

To further understand the floater strategy, one first needs to consider the question 'Why float instead of remaining to help on the natal territory?' A poor quality natal territory may not be worth inheriting. Additionally, a large group size would increase the time spent waiting to inherit the natal territory and/or limit resources available to additional helpers – both of which could cause a fledgling to disperse and become a floater. While dispersal poses a greater survival risk (Daniels and Walters 2000), floaters may offset this cost by obtaining a breeding vacancy sooner or on a higher quality territory than their natal site.

One must next contemplate 'Why affiliate instead of continue to search for a vacancy?' As stated above, by affiliating with a particular territory, an individual becomes familiar with the territory, which could result in an enhanced probability of survival and a better position from which to evict a breeder or bud. Alternatively, a floater might benefit by continuing to search for a vacancy by monitoring a wider ranger of territories, thus increasing its chances of detecting a vacancy; however, unaffiliated floating could be riskier in terms of decreased survival probability and diminished familiarity with an area. Searching and waiting for a vacancy could also be less costly than fighting with group members; but an unaffiliated floater of poor individual quality may just be more easily repelled by groups and unable to establish itself as an affiliated floater. Thus, unaffiliated floating may not be a choice.

Lastly, why help unrelated individuals instead of being an affiliated floater? Dispersers sometimes, albeit rarely, become unrelated helpers (Walters et al. 1988, Walters 1990). In my

dataset only 12 individuals became unrelated helpers, which represents only 0.31% of bird-years. All but one helped for only one year. The twelfth bird helped for two consecutive years, but on two different territories. Furthermore, all but one helped on territories that had only a breeding pair, thereby assuming the dominant helper position. Helping non-relatives is extremely costly as no indirect fitness benefits are accruing. Unrelated helpers could exist as an application of the pay-to-stay hypothesis (Kokko et al. 2002). But then why not attempt to affiliate with another territory? Perhaps dispersers choose to help nonrelatives on high quality territories. While a high quality territory is needed to support a large group, small groups do not necessarily inhabit low quality territories.

Further topics to consider are whether floaters, like unrelated helpers, choose smaller groups with which to affiliate and whether unrelated helpers (and possibly affiliated floaters) choose smaller groups because of less resistance by resident birds or because it gives them a greater probability of obtaining that breeding vacancy when the breeder dies. Comparing lifetime reproductive success among unrelated helpers, and affiliated and unaffiliated floaters could answer many of the aforementioned hypotheses.

Comparison with Other Cooperative Breeding Species

I reviewed the cooperative breeding literature and discovered only seven species that have been documented to form new territories by budding or pioneering: Red-cockaded woodpeckers (Walters et al. 1988, Walters 1991), Florida Scrub Jays (*Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1978, 1984), Seychelles Warblers (*Acrocephalus sechellensis*, Komdeur and Edelaar 2001*ab*), Hoatzins (*Opisthocomus hoatzin*, Strahl and Schmitz 1990), Laughing Kookaburras (*Dacelo novaeguineae,* Legge and Cockburn 2000), Brown Treecreepers (*Climacteris picumnus*, Walters et al. 1999), and Superb Fairy-wrens (*Malurus cyaneus,* Cockburn et al. 2003). Given that many cooperatively breeding species are generally described as having a shortage of breeding vacancies, I suspect that territorial budding is both under-studied and under-reported. Including my study, young males almost exclusively perform territorial budding – regardless of whether males are the primary helper sex. The two exceptions are female Superb Fairy-wrens, which apparently initiate budding by pairing with a helper male (Cockburn et al. 2003), and Laughing Kookaburras where males and females both help and bud (Legge and Cockburn 2000).

This male bias in budding behavior may result from increased testosterone and aggression in males. While male Hoatzin helpers are more active than female helpers in providing assistance, some contribute more than the breeders, others less (Strahl and Schmitz 1990). It is unclear whether helpers give more or less assistance equally to helping duties such as territory defense and aid to young. Additionally, immigrants help little, but more often assist with territory defense. Thus, it is apparent that a range of territorial aggression exists and possibly contributes to which males bud. Furthermore, Seychelles Warblers future (male) budders had significantly more aggressive interactions with their neighbors compared to future helpers, floaters, and breeders (budders, helpers, and floaters do not switch between these strategies; Komdeur and Edelaar 2001*b*). These future budders also assisted significantly more with territory defense than these other classes. Thus, perhaps individual quality in terms of aggression and fighting ability contribute to which males bud in Red-cockaded woodpeckers and other cooperative breeding species.

In all of these species except the Seychelles Warbler, budding males are often former helpers. Also, male Seychelles Warblers and Florida Scrub Jays always bud from their natal territories (Komdeur and Edelaar 2001*ab*, Woolfenden and Fitzpatrick 1978, 1984). So why did Red-cockaded woodpecker helpers pioneer in proportion to their frequency in the population, and why did helpers more often bud from a non-natal territory? Furthermore, my analyses revealed that helper dominance rank was not related to territory creation events. Why would a dominant helper abandon his status as next in line for a breeding vacancy and bud from another territory or pioneer? The answer could be lack of complete habitat saturation. In Red-cockaded woodpeckers, there could be an indirect and direct fitness cost to splitting the natal territory. A smaller territory could result in decreased group size and number of fledglings for both the budder and its father. Unlike Red-cockaded woodpecker parents, Seychelles Warbler (Komdeur and Edealaar 2001*a*) and Florida Scrub Jay (Woolfenden and Fitzpatrick 1984) parents help their offspring enlarge the natal territory prior to budding; although Woolfenden and Fitzpatrick (1984) acknowledge that it is unclear whether territory expansion allows budding to occur or whether incipient budding causes territory expansion. If the former is true, perhaps this parental helping behavior is an adaptation to complete habitat saturation, whereby a parent increases its genes in a population via its offspring by assisting them in acquiring a breeding position. While productivity may decline with decreasing territory size, as in Seychelles Warblers for example

(Komdeur and Edelaar 2001*a*), by helping its offspring enlarge the natal territory, a parent could offset this cost by having the collective fitness benefits (breeder plus offspring) from two smaller territories outweigh the direct fitness benefits of the breeder on a larger territory. It would be beneficial to look at the inclusive benefits from a parent's point of view and calculate lifetime reproductive success including the fitness benefits gained by offspring of parents who help enlarge the natal territory versus those that do not. This parental helping strategy might be optimal in species constrained by absolute habitat saturation, like Florida Scrub Jays and Seychelles Warblers, but possibly not so for Red-cockaded woodpeckers. Since Red-cockaded woodpeckers can pioneer new territories and bud from existing territories possibly without impacting neighboring territories much (it is unclear to what extent budding affects neighboring territories), perhaps parents and offspring are better served by not splitting the natal territory. Further support for this parental behavior hypothesis comes from Cockburn et al. (2003), who speculate that breeding female Superb Fairy-wrens initiate divorce once their sons reach the breeding or dominant helper position to relieve constraints on recruiting sons in the local area.

Red-cockaded woodpeckers are unique because as long as habitat is otherwise suitable – old pines, low-density hardwoods, abundant groundcover – they can create new territories by excavating new cavity trees via pioneering without significantly affecting neighboring territories. Both Seychelles Warblers and Florida Scrub Jays occupy completely saturated habitat – no habitat remains in which to establish a new territory by pioneering. Rather, any new territory that is created is done through budding at the expense of neighboring territories. Red-cockaded woodpeckers are also unique because once a territory has budded it remains a stable territory. Seychelles Warbler and Florida Scrub Jay territories that are created by budding are sometimes temporary. Seychelles Warblers appear to use the budded territory as a staging ground for inheriting the natal territory, although the budded territory does sometimes become permanent if sufficiently enlarged (Komdeur and Edelaar 2001*b*). Similarly, Florida Scrub Jay territories seem to undergo fusion and fission in response to changing group sizes.

These unique traits of Red-cockaded woodpeckers, however, may apply only to the species' history of habitat degradation; i.e. these traits may be operationally, but not inherently, unique. Once complete habitat saturation occurs – with cavity trees saturating suitable habitat – Red-cockaded woodpeckers will no longer be able to create new territories via pioneering. With budding the only option remaining to create new territories, territory sizes could vary from year

to year and budded territories could become more ephemeral. Thus, the time to use this information for conservation purposes is now. There is the potential to use budding and pioneering to naturally grow populations now, but perhaps not in the future.

Management Recommendations

To increase Red-cockaded woodpecker populations naturally through budding and pioneering, a greater number of young, male nonbreeding individuals are needed. More floaters and larger group sizes resulting from additional helpers also means increased competition, and thus more territory creation events. Heppell et al (1994) modeled management alternatives for Red-cockaded woodpeckers using a stage-based matrix model and concluded that improving habitat quality and providing recruitment clusters would increase the number of territories, whereas increasing survival or fecundity would only augment helper class numbers. They also stated that density-dependent effects (resulting from a larger helper class) are unknown; however, it appears from this study that increased rates of budding and pioneering are the result. However, rather than establish how to increase survival and fecundity, I support a long-term, ecosystem-level approach that centers on habitat improvement through the use of prescribed growing-season fire that has been advocated elsewhere (Conner et al. 2001, James et al. 2001, Taylor 2003, USFWS 2003).

The longleaf pine ecosystem, with which Red-cockaded woodpeckers are strongly associated, is dependent on frequent (1-6 years), low-intensity fires to maintain an open midstory (Frost 1998; for a comprehensive review of the role of fire in the longleaf pine ecosystem see Conner et al. 2001, Taylor 2003). Historically, many of these fires likely originated from lightning strikes, and thus occurred during the growing season, when lightning is common (Frost 1998, Conner et al. 2001). High-quality habitat for Red-cockaded woodpeckers (which likely coincides with the historical structure of longleaf pine forests) consists of old-growth pines in at least low densities, intermediate densities of medium-sized and large pines, and sparse or no hardwood midstory (Walters et al. 2002a). Abundant herbaceous ground cover is also an integral component of high-quality habitat (James et al. 1997, 2001). Fire suppression policies that allowed scrub oak species (*Quercus* spp.) to reach the midstory have caused Red-cockaded woodpeckers to abandon their cavities (Conner and Rudolph 1989). Fire reduces hardwood midstory and results in a more diverse herbaceous groundcover.

Improving habitat quality through growing-season prescribed fire serves two purposes regarding territory creation events. First, suitable habitat is necessary for a bird to bud or pioneer. Second, several connections have been established which together suggest that arthropods originating in the groundcover (which is improved by fire) increase Red-cockaded woodpecker productivity. Arthropod prey of Red-cockaded woodpeckers, found on tree boles, originates from the forest floor (Hanula and Franzreb 1998). While Hanula and Horn (2004) found no relationship between herbaceous groundcover and arthropod abundance on tree boles, Taylor (2003) controlled for tree species, tree age, soil type, hardwood midstory density, and overstory basal area and found otherwise. He documented a significant and positive association of arthropod biomass with the percent cover of herbaceous and graminoid components in the groundcover and a significant and negative relationship to woody vegetation (Taylor 2003). James et al. (1997, 2001) have documented increased Red-cockaded woodpecker group size, group density, and productivity with both a larger proportion of wiregrass and a lower proportion of woody vegetation in the groundcover. Similarly, Hardesty et al. (1997) discerned that 35% of the variation in Red-cockaded woodpecker productivity was explained by increased forb cover, while 28% of the variation was explained by reduced hardwood midstory. Likewise, Walters et al. (2002a) determined that smaller groups sizes were associated with territories having larger amounts of hardwood midstory. While the link between increased arthropod biomass and larger groups and productivity remains to be demonstrated, the growing body of literature is extremely suggestive that prescribed growing-season fire produces more Red-cockaded woodpecker fledglings via improved groundcover and increased arthropod biomass and could result in an augmented nonbreeding population – necessary for increased budding and pioneering rates. That Red-cockaded woodpecker territories are aggregated around impact areas on military installations, where fires are commonly ignited from munitions, provides further evidence that fire is beneficial to this species (Conner et al. 2001, USFWS 2003). On Camp Lejeune, 26 of the 81 occupied territories are clustered around the G-10 impact area (Fig. 1). In addition, 6 of the 11 territories split by budding were located around the G-10 impact area, suggesting that high quality habitat stimulates budding.

Heppell et al. (1994) also advocated the creation of new territories using artificial cavity techniques. However, recruitment clusters actually impede natural population growth because they draw in helpers and floaters, thus reducing the number of nonbreeding individuals,

competition, and consequently the number of buds and pioneers. Conner et al. (2002) described a decreased rate of cavity excavation in longleaf pines when artificial cavities were regularly installed. Anecdotally, the number of buds and pioneers decreased after recruitment clusters were installed on Camp Lejeune (Fig. 5). Regardless of actual cost, there is a needless opportunity cost to other activities and species of continuing artificial cavity construction when not needed. I am not advocating abandoning the installation of recruitment clusters for supporting critically small populations. I am suggesting restricting use of artificial cavities to installing recruitment clusters in small populations (<30 groups; USFWS 2003) and to augment existing clusters as needed (to maintain four suitable cavities per cluster), as long as suitable old pines exist in which Red-cockaded woodpeckers can create their own cavities naturally. Otherwise, devoting time and resources to ecosystem management of longleaf pine forests, a large component of which is prescribed growing-season burning, would not only benefit Red-cockaded woodpeckers but all species in this ecosystem.

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Fig. 2.1. Map of Marine Corps Base Camp Lejeune, North Carolina, showing major training areas. Black polygons portray red-cockaded woodpecker clusters with buffer zones 1988-2005.
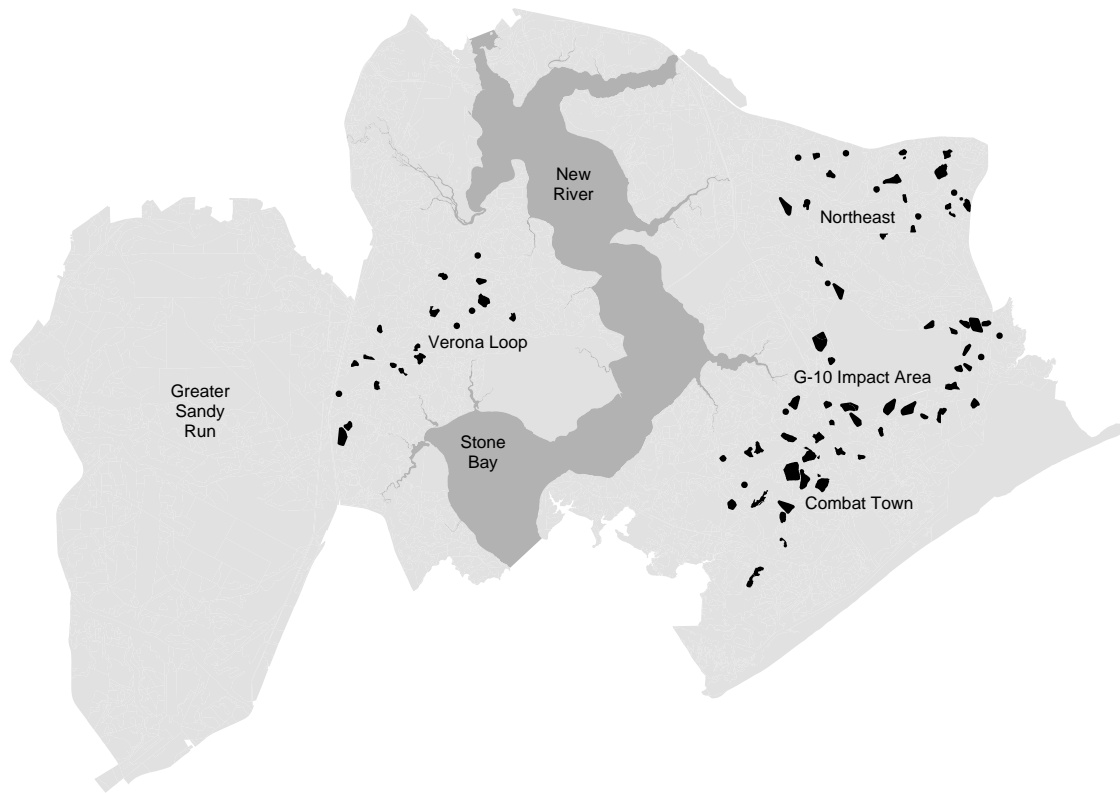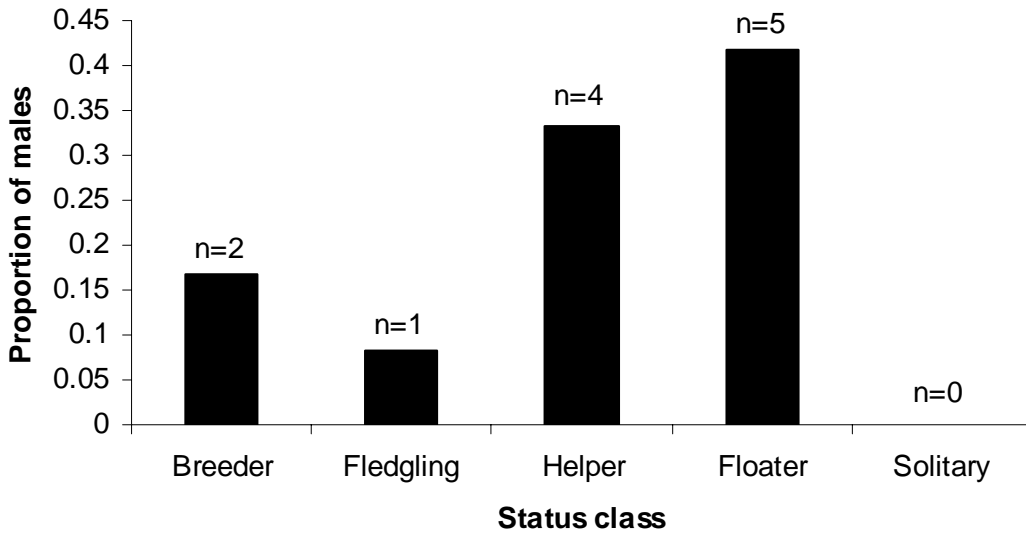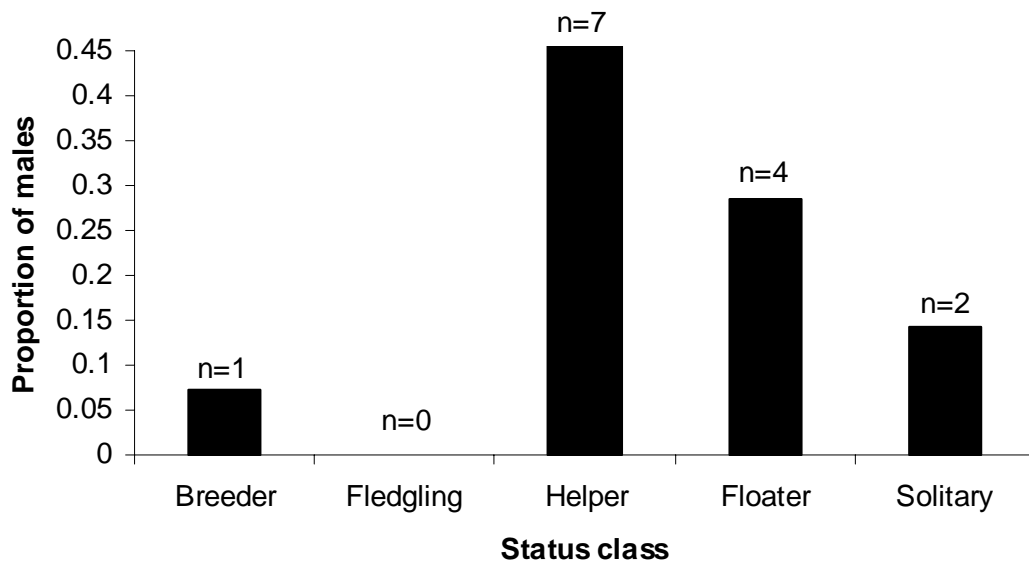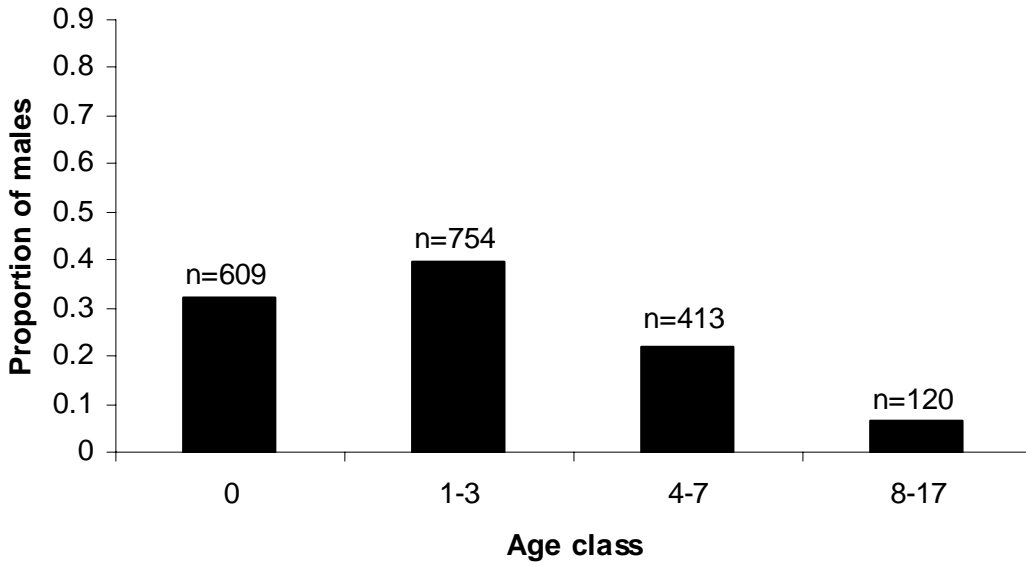
Fig. 2.2. Comparison of (A) the proportion of males in each status class in the population with the proportion of males in each status class that (B) budded or (C) pioneered on Camp Lejeune, North Carolina 1988-2005. Sample sizes are indicated above the bars and designate (A) bird-years and (B-C) the number of birds that (B) budded or (C) pioneered.
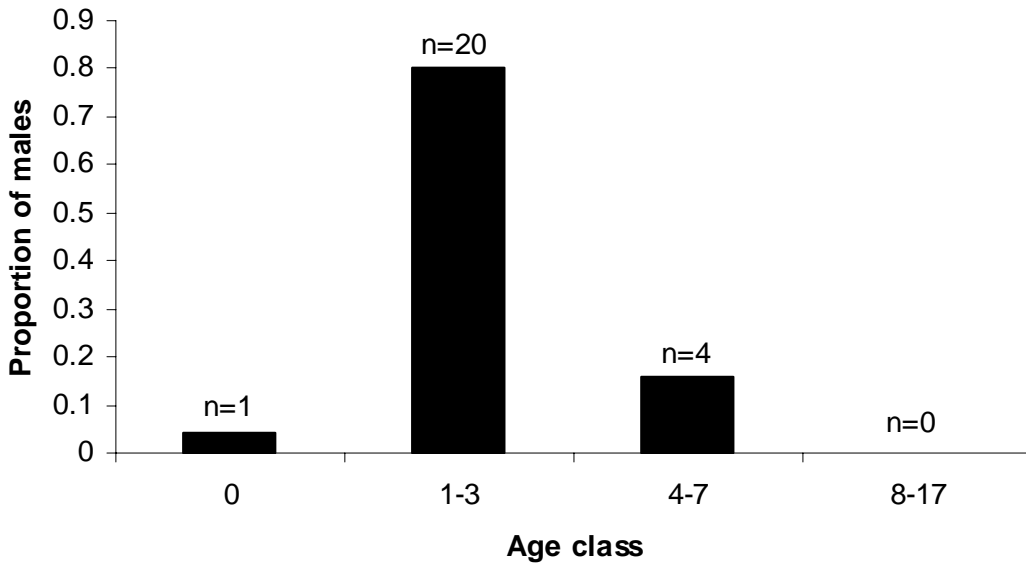
(A)
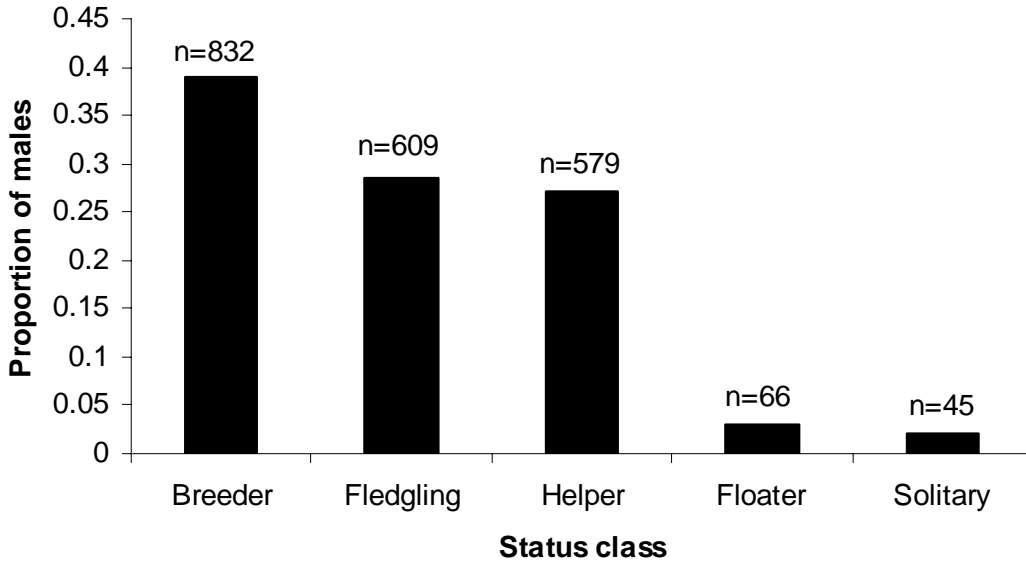
(B)

(C)

Fig. 2.3. Comparison of (A) the proportion of males in each age class in the population with (B) the proportion of males in each age class that budded or pioneered on Camp Lejeune, North Carolina 1988-2005. Sample sizes are indicated above the bars and designate (A) bird-years and (B) the number of birds that budded or pioneered.
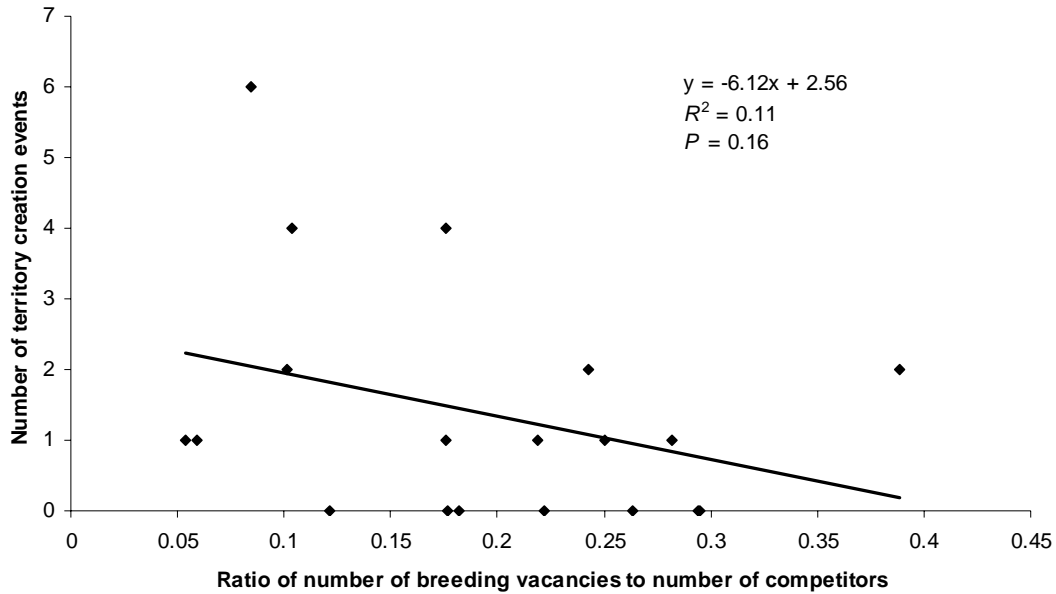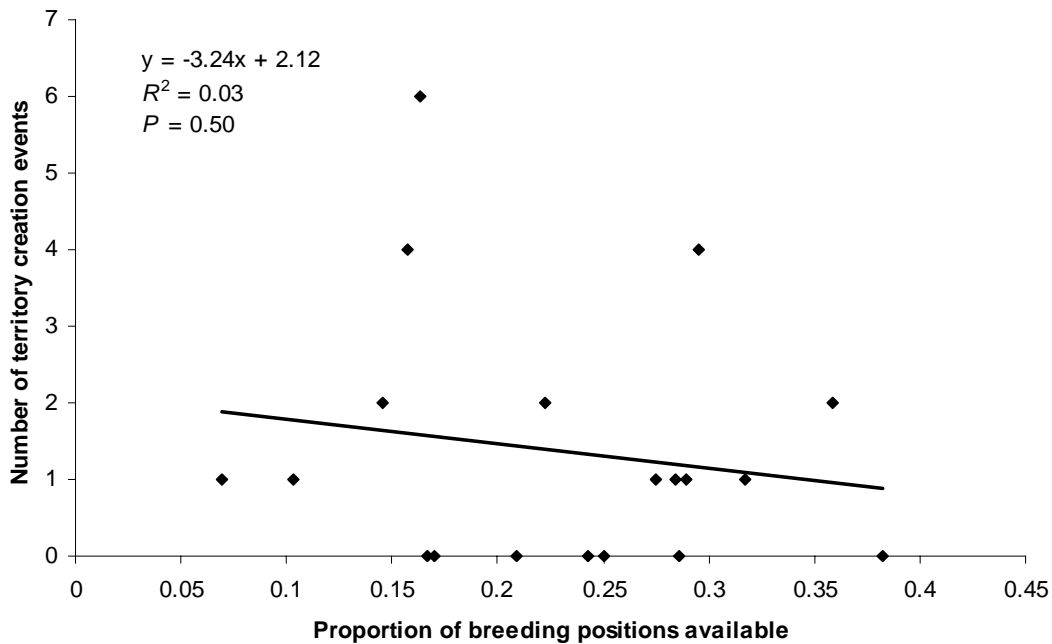(A)

(B)

Fig. 2.4. Comparison of the combined number of budding and pioneering events with (A) the ratio of the number of breeding vacancies to the number of competitors, (B) the proportion of breeding positions available, (C) the proportion of the population comprised of competitors, and (D) the proportion of females available on Camp Lejeune, North Carolina 1988-2005.
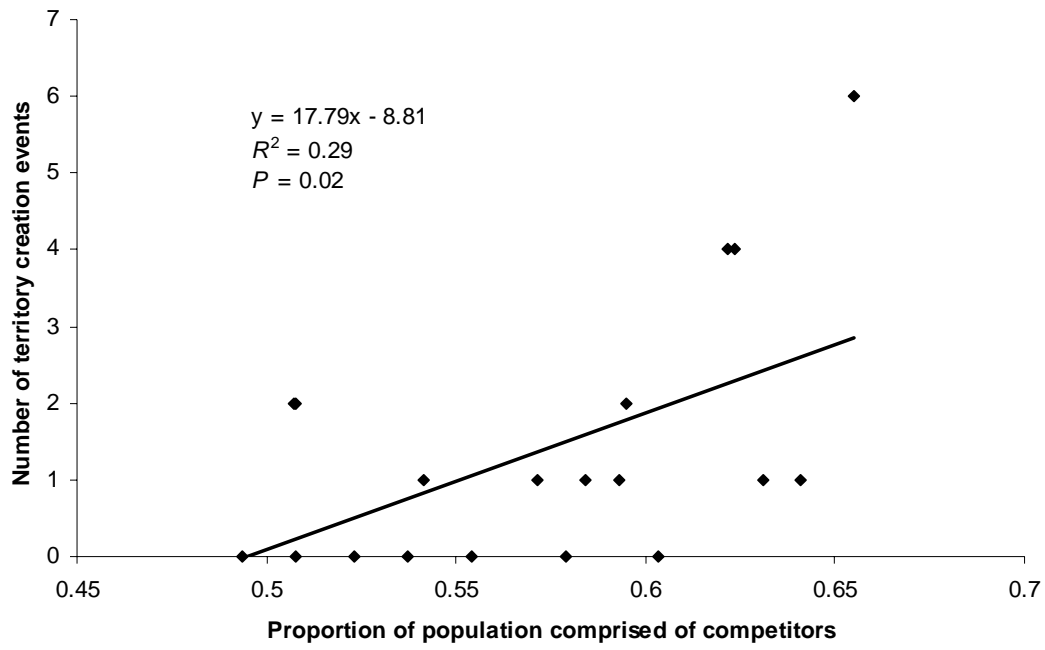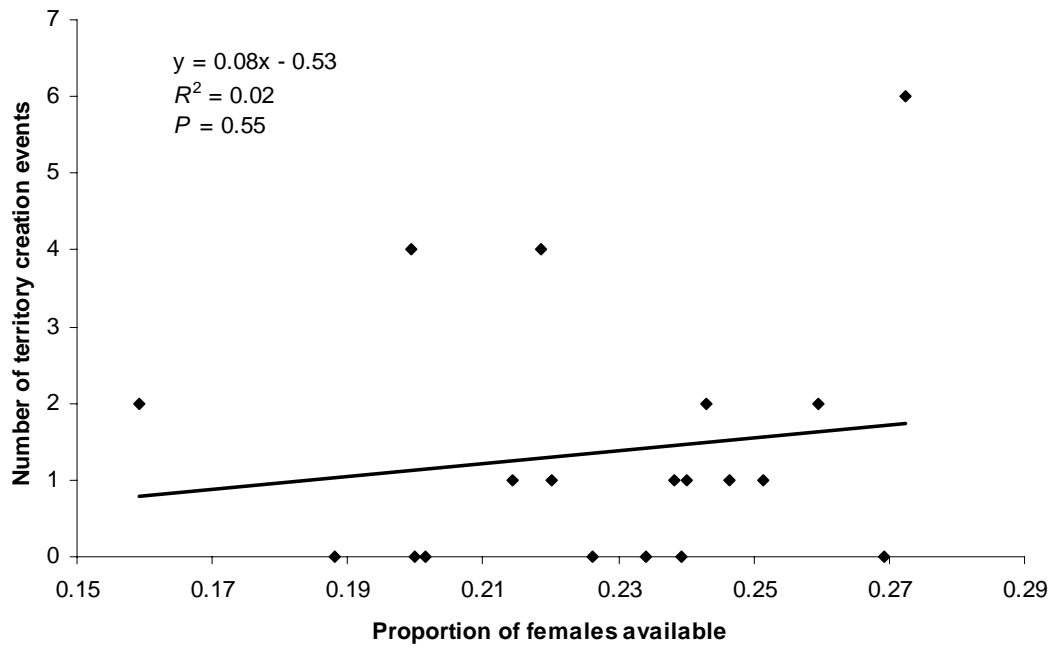
(A)

y = -6.12x + 2.56
R^2 = 0.11
P = 0.16

(B)

y = -3.24x + 2.12
R^2 = 0.03
P = 0.50

(C)

$y = 17.79x - 8.81$
$R^2 = 0.29$
$P = 0.02$

Number of territory creation events

Proportion of population comprised of competitors

(D)

$y = 0.08x - 0.53$
$R^2 = 0.02$
$P = 0.55$

Number of territory creation events

Proportion of females available

Fig. 2.5. Comparison of the number of budding and pioneering events each year with the number of recruitment clusters created on Camp Lejeune, North Carolina 1988-2005.