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CONSISTENCY OF OVENBIRDS IN A CONTIGUOUS FOREST

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ABSTRACT

Birds likely have evolved behavioral adaptations that allow them to recognize suitable habitats to improve their chances of reproducing, and past studies indicate that reproductive failure may encourage dispersal. I investigated habitat selection patterns of 132 uniquely color-banded male Ovenbirds (*Seiurus aurocapilla*) at Hawk Mountain Sanctuary in eastern Pennsylvania to determine if territory quality could be estimated reliably using measures of occupancy. Furthermore, I tested whether returns and territory shifts were associated with prior reproductive success and bird age. I measured occupancy as the number of birds that occupied 30-m grid cells that covered two 18-ha study sites over the 12-year period and similarly calculated reproductive success rates within each grid cell. I measured first-year return rates and used GIS to calculate shift distances and overlap between consecutive territories. Despite variation in occupancy, reproductive success rates were generally high. Return rates also were high and birds rarely moved more than a territory width (68 m) during their lifetimes. There was no relationship between site fidelity and past reproductive success, but shift distances decreased with age. My results differed from past studies that found a relationship between breeding dispersal and past reproductive success for species in a number of habitats. The lack of territory movements of Ovenbirds at Hawk Mountain Sanctuary may represent a general case for songbirds breeding in stable, high quality habitats, where sources of failure are infrequent and unpredictable. Birds may base dispersal decisions on more than personal breeding experience by monitoring the performance of neighbors to make broader assessments of habitat quality, which could explain why patterns of fidelity differ among habitats based on quality and level of heterogeneity.

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INTRODUCTION

Resource variation among habitats can influence the reproductive performance of individuals and populations resulting in trends whereby habitats with a favorable combination of resources are consistently more productive over time. Thus, for highly mobile organisms, there is considerable selective pressure on individuals to be able to assess conditions and make habitat choices meant to maximize relative fitness. These notions are the evolutionary underpinnings of habitat selection theory which, restated in the proper terminology, assumes that habitats differ in quality (or suitability) and individuals behave in an "ideal" fashion (Fretwell and Lucas 1970), always selecting the habitat that maximizes their chances to survive and reproduce. Researchers often attempt to identify factors that account for the disproportionate use of certain habitats and, ultimately, the success of individuals within those habitats. Such studies provide scientists and land managers with a better understanding of complex adaptive behavior and specific information on the resource needs of wildlife species used for conservation planning.

Birds have been at the center of habitat studies since Grinnell (1916) and Lack's (1933) early investigations into the environmental factors that influence local abundance and geographic distributions. Their prominent role likely originates from naturalists' penchant for noting features at sites where they collected specimens, but it also may be a consequence of the conspicuous nature of birds, which allows for efficient data collection (Block and Brennan 1993). In the case of migratory bird species, habitat selection is of considerable importance because individuals must make habitat choices many times during a short lifespan as they travel hundreds of miles between wintering and breeding grounds and feed in stopover sites along the way. Additionally, individuals that manage multiple breeding attempts may make adjustments

within or between seasons as they must decide whether to return to sites they occupied previously or disperse in search of a better locale.

The primary theoretical models of habitat selection, the ideal-free and ideal-dominance distributions, provide a framework for measuring habitat quality by making among habitat comparisons of average fitness measures, which often are estimations of population parameters such as rates of reproduction and survival (Fretwell and Lucas 1970, Johnson 2007). Under the ideal-free distribution, equally competitive individuals settle into the highest quality habitat until density-dependent effects reduce average fitness to the level of the next best habitat, when individuals settle into both habitats at an equal rate. The ideal-dominance distribution or the conceptually similar ideal-preemptive distribution (Pulliam and Danielson 1991) assumes that dominant competitors are able to exclude subdominants, forcing them to occupy lesser quality habitats before they would under the ideal-free model. Thus, under the ideal-free distribution, fitness measures are the same among habitats and density is an accurate predictor of quality; whereas under the ideal-dominance distribution fitness measures decline in a direct relationship with habitat quality, which cannot be predicted reliably using density alone (Van Horne 1983).

Comparisons of populations in different habitat types have provided considerable support for the ideal-dominance selection model. Holmes et al. (1996) found Black-throated Blue Warblers (*Dendroica caerulescens*) were more productive and lived at higher densities in New Hampshire forests with a dense shrub stratum; whereas forests with a sparse shrub layer were composed of a higher proportion of young males. Petit and Petit (1996) reported similar findings for Prothonotary Warblers *(Protonotaria citrea)* in Tennessee, where older and brighter males settled in the better, flooded habitats before younger males established territories in worse, dry habitat. Similar patterns occur in fragmented landscapes where differences in breeding success,

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survival, and age structure are related to patch size for area-sensitive species such as the Wood Thrush (*Hylocichla mustelina*, Hoover et al. 1995) and Ovenbird (*Seiurus aurocapilla*, Porneluzi et al. 1993, Villard et al. 1993, Burke and Nol 1998, Porneluzi and Faaborg 1999, Bayne and Hobson 2001).

Obtaining demographic measurements generally requires intense effort on the part of researchers because of logistic difficulties inherent in following marked individuals on study sites to determine outcomes of breeding attempts or rates of return adequate for analysis (Johnson 2007). When researchers have a thorough understanding of the resource needs of a species, they can estimate habitat quality by measuring resources directly (Cody 1981, Smith and Shugart 1987, Orians and Wittenberger 1991, Rodenhouse et al. 2003); however, this approach can require the same level of effort used to estimate population parameters and the accuracy of measurements may be questionable (Hutto 1990).

A different set of methods extends the assumption of ideal selection behavior and assesses habitat quality using the distribution of individuals to test for the disproportionate use of habitats (Garshelis 2000). Dependent variables may be the relative amount each habitat is used, presence-absence (Thompson and Capen 1988) or presence-only data (Dettmers and Bart 1999, Tapia et al. 2007), or the frequency of use (i.e. occupancy) over time (Møller 1982, Matthysen 1990, Arlt and Pärt 2007). A number of circumstances may promote selection of poor habitats (Railsback et al. 2003, Battin 2004), potentially leading to spurious results if only distributional measures are used; however, Sergio and Newton (2003) found occupancy to be a reliable predictor of productivity and other demographic measures of habitat quality. Unfortunately, the long study lengths needed to identify how occupancy varies among habitats negates the relative

ease in determining use during a single season (e.g. 17 of 22 studies reviewed by Sergio and Newton [2003] lasted at least seven years and as many as 32 years).

Researchers typically use the density-dependent habitat models (i.e. ideal-free and ideal-dominance distributions) to interpret patterns of selection at large spatial scales; however, animals make smaller-scale habitat choices as they establish territories, nesting locations, and feeding sites (Johnson 1980). Studies addressing selection at this level (termed microhabitat selection) rely heavily on habitat use measures, which investigators often relate to resources, vegetation, and other habitat features (Wiens et al. 1986, Ens et al. 1992, Hoover and Brittingham 1998, Barg et al. 2006, Arlt and Pärt 2007, Senner et al. 2009). For example, Smith and Shugart (1987) found prey density to be highly correlated with habitat structure, which was a reliable predictor of habitat use and territory size for Ovenbirds in eastern Tennessee. Such descriptive studies can be time and site-specific (Collins 1983, Morrison 2001), especially when researchers fail to replicate over time and space (Hurlbert 1984). In fact, the relationship between habitat structure and Ovenbird use in Tennessee contradicted that reported by Stenger and Falls (1959) in southern Ontario.

Many studies have reported differences in reproductive success related to age and general condition of individuals (Hamilton and Zuk 1982, Pugesek 1983, Wheelwright and Shultz 1994, Forslund and Pärt 1995). Thus, variation in bird quality can confound assessments of habitat quality based on demographic measures, and investigations conducted at the level of territories are particularly vulnerable because researchers cannot average measures among individuals within the same habitat unless they collect data over multiple seasons. Moreover, considerably long study lengths often are necessary to overcome additional concerns raised by resampling individuals, which often occurs due to high rates of site fidelity of many bird species.

Cases in which birds returned to previous territories following drastic habitat alterations (Hildén 1965, Wiens et al. 1986) have led some researchers to consider site fidelity to be a rigid behavior that counteracts "ideal" habitat selection in older individuals (Johnson 2007); however, there is strong evidence that the decision to return or move away (disperse) from a former site is the result of adaptive responses to habitat conditions. Reusing a former territory reduces search costs (Stamps et al. 2005), such as risk of mortality or time that could have been allocated to breeding activities, and familiarity may enable individuals to use resources efficiently and provide advantages during defense assuming habitat conditions are relatively stable over time (Greenwood and Harvey 1982). For individuals occupying low quality sites, however, it may be beneficial to endure search costs to find a better location. The "decision rules" hypothesis states that birds use past experience to decide which strategy to employ, thus explaining observations that birds that fail to produce young during one year return to the same breeding site the next year at lower rates or disperse farther than birds that bred successfully (Harvey et al. 1979, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Payne and Payne 1993). Experiments manipulating breeding success provide strong support for a causal link between failure and dispersal (Bollinger and Gavin 1989, Haas 1998, Hoover 2003).

Studies following between-year territory shifts have found that birds frequently choose sites with higher occupancy scores than their previous one, and these sites tend to have higher long-term measures of productivity or reproductive success (Krebs 1971, Møller 1982, Beletsky and Orians 1987, Matthysen 1990, Forero et al. 1999, Sergio and Newton 2003, Espie et al. 2004). Older birds show higher rates of fidelity than younger birds (Harvey et al. 1984, Montalvo and Potti 1992, Newton 2001), which may be an indication that individuals are reluctant to move once they find a suitable site. Furthermore, Bollinger and Gavin (1989)

reported Bobolinks (*Dolichonyx oryzivorus*) on a productive site returned at high rates that were independent of breeding success the previous year, which departed from the pattern observed on lower quality sites. Therefore, birds may use information in addition to that obtained through personal breeding experience when evaluating habitats to decide whether to reuse former sites or disperse, further suggesting that they respond to variation in habitat quality in an ideal manner.

I investigated territory-level habitat selection patterns of Ovenbirds (*Seiurus aurocapilla*) using measures of habitat use, reproductive success, and local dispersal resulting from between-year movements of individuals collected over a 12-year period from a population of uniquely color-banded males at Hawk Mountain Sanctuary in eastern Pennsylvania. My primary goals were to use this unique long-term dataset to test hypotheses concerning ideal selection behavior as well as to describe territory fidelity behavior of an area-sensitive Neotropical migrant by quantifying year-to-year movements of several generations of individuals over the course of their lifetimes. In particular, I hypothesized that individuals would show preference for the most suitable territories and that returns and patterns of local dispersal would be associated with prior breeding success. Therefore, I predicted that occupancy would vary over my study sites based on differences in suitability among territories and that occupancy would have a positive relationship with site-specific measures of reproductive success. I further tested whether I could predict occupancy or reproductive success reliably based on habitat features using *a priori* candidate models. Finally, I predicted individuals would have a greater tendency to disperse following reproductive failure and that older individuals would have higher rates of site fidelity.

METHODS

Study sites

My study was conducted at two forested sites, Owl's Head (OH) and River of Rocks (RR), at Hawk Mountain Sanctuary (40º 38'N and 75º 59'W) in eastern Pennsylvania (Fig. 1A). Conservationists founded the sanctuary in 1934 to protect migrating raptors along the Kittatinny Ridge and it is part of a 10,000-ha tract of second growth mixed-deciduous forest comprised of public and private lands. Hawk Mountain Sanctuary researchers established the study sites as Breeding Bird Census (BBC) plots in 1982 to monitor bird diversity (Goodrich et al. 1998). The sites are 1.5 km apart and each contains grid points (238 and 210 at Owl's Head and River of Rocks, respectively) marked at 30.5 m intervals (Fig. 1B). Owl's Head (490 × 400 m, 19.4 ha) sits at an elevation of 440 m on the southwest-facing mountainside; whereas, River of Rocks (430 × 400, 16.9 ha) sits on the east-facing side of the ridge and varies in elevation from 275-335 m (Goodrich et al. 1998).

There are considerable structural differences between sites. Owl's Head has a more gradual slope, lower canopy height, higher shrub density, and more small trees occupying space in the understory than River of Rocks, which has lower vegetative ground cover and higher rock cover. Dominant overstory species at both sites include chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), red maple (*Acer rubrum*), scarlet oak (*Q. coccinea*), sweet birch (*Betula lenta*), and white oak (*Q. alba*). Pitch pine (*Pinus rigida*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*) occur in low densities. The shrub layer is composed of huckleberry (*Gaylussacia baccata*), blueberry (*Vaccinium* spp.), sheep laurel (*Kalmia augustifolia*), mountain laurel (*K. latifolia*), and wintergreen (*Gaultheria procumbens*). Canopy trees at both sites range

in age from 120 to 200 years, and excluding a 0.8-ha section of OH that was cut in the mid-1970s, the sites have remained relatively undisturbed over the last century (Goodrich et al. 1998).

Study species

The Ovenbird is a Neotropical-Nearctic migrant that breeds throughout much of North America and spends the non-breeding season in southern North America, Central America, and the Caribbean Islands (Van Horn and Donovan 1994). In Pennsylvania, Ovenbird males arrive in late April and establish territories before females arrive approximately one week later (Porneluzi et al. 1993, Goodrich et al. 1998). Males display territorial behavior through morning song and give chase to intruding males (Hann 1937, Van Horn and Donovan 1994). Territories remain fixed throughout the breeding season, but territorial defense is less rigorous late in the season when fledglings leave the nest (Hann 1937, Stenger and Falls 1959). Females build nests on the ground and lay eggs in May, which hatch from late May through June. Ovenbirds are single-brooded, but they may renest after failure (Van Horn and Donovan 1994). Clutch sizes range from three to six eggs and males do not help with incubation (Van Horn and Donovan 1994). Fledglings leave the nest approximately eight days after hatching and are semi-dependent for 30 days (Hann 1937). During this fledgling period, which spans from mid-June through mid-July, fledglings can be observed in close association with parents (Porneluzi et al. 1993).

Bird censuses

Hawk Mountain Sanctuary researchers began color-banding male Ovenbirds in 1988 using OH and RR as control sites for a large-scale study investigating population dynamics in a

fragmented landscape (Porneluzi et al. 1993, Goodrich et al. unpublished data). Researchers stopped banding at all sites in 1996 following completion of the forest fragmentation study. Banding resumed at OH and RR in 1998 and data collection continued at only these sites through 2009. I chose to use the final 12 years for my study period because the consistency in data collection allowed for comparisons among years and I avoided complications arising from the pause in banding during the 1996 and 1997 seasons. During the 12-year study period, there were 132 banded (76 OH, 56 RR) and 47 unbanded (30 OH, 17 RR) male birds on the study sites.

Researchers trapped males early in the breeding season using mist-nets and song playback accompanied by a wooden decoy. Birds were aged as either second-year (SY) or after second-year (ASY) birds according to plumage coloration and rectrice shape (Pyle et al. 1987). Each bird received an aluminum U.S. Fish and Wildlife Service band with three color bands in a unique combination (Banding Permit Number 22749, Institutional Animal Care and Use Committee Number 28329). Throughout the breeding season, from May through mid-July, researchers conducted bird censuses from approximately 0530 to 1000 several mornings per week by spot-mapping the locations of singing males and observing their behavior. Spot-mapping is a technique whereby observers use grid markings in the field (flagging tape on trees) to plot locations of birds identified by band combination on a map of the study site (Bibby et al. 1992). Each bird census covered an entire study site and researchers visited territories at different times in case activity of individuals varied temporally.

Limited person power (i.e. the three years I worked on the study were the only years with two full-time researchers) and time prevented researchers from locating and determining the fate of every nest. Instead, researchers visited each territory approximately every four days during the fledgling period (from early June through mid-July) and classified birds as "successful" if

banded adults were observed feeding, defending, or interacting closely with at least one fledgling. Porneluzi et al. (1993) noted this method estimates a minimum success rate as some individuals with fledglings may move off study sites and escape detection. To reduce this bias, I classified birds as "unsuccessful" if they were not observed with fledglings after a minimum of three observations during the fledgling period. I considered birds not observed the minimum number of times to have "unknown" reproductive status and excluded them from analyses based on reproductive success. The three observation minimum was an appropriate cutoff because nearly one-third (74/242) of successful birds were observed fewer than three times during the fledgling period and many birds above the minimum were observed several times after being found with fledglings.

Habitat measures

To measure habitat use and patterns of reproductive success at different locations on each site, I used a Trimble TDC1 Data Collector (Trimble Navigation Limited™) GPS device to collect GPS coordinates of the grid points used for spot-mapping and plotted bird locations from every season onto maps of the study sites using the editor toolbar in ArcMap (ArcGIS version 9.2, ESRI Inc., Redlands, CA). I only plotted locations of birds that were observed on three separate occasions and were located within site boundaries at least once. I used Hawth's Tools (Beyer 2004) to construct a grid over both study sites using cell widths of 30.5 m (distance between spot-mapping grid points) and calculated a within-season measure of use based on the number of different birds that were located within a grid cell during a season. Occupancy was calculated by summing the within-season measures over the 12-year study period (units = total bird-years). I calculated rates of reproductive success (success rates) at each grid cell by finding

the mean success rate of all birds with known reproductive status that occupied a particular cell over the study period. Individuals that returned to the same cell multiple years were resampled. I calculated Pearson's product-moment correlation coefficient between occupancy and success rates and tested for a correlation using the null hypothesis that the variables were uncorrelated (Sokal and Rohlf 1995).

During the summer of 2008, I systematically sampled habitat variables at both sites using every spot-mapping grid point as a sampling point and a modification (Martin et al. 1997) of the methods of James and Shugart (1970). Each grid point served as the center of an 11.3-m radius circular plot and a nested 5-m radius circular plot that was divided into 4 quadrants. From the plot center, I measured canopy cover (%) using a densiometer and canopy height (m) and slope (degrees) using a clinometer. I used the large plot to measure density (stems per 100 m^2) of small trees (<23 cm DBH), large trees (>23 cm DBH), conifers, and snags. The small plot was used to measure shrub density (stems per 10 m^2), litter depth (mm), and ground cover (%) ocular estimates in 13 categories: bare, brush, fern, forb, grass, green (i.e. total vegetative ground cover), litter, log, marsh, moss, rock, shrub, and water.

Unfortunately, the RR grid constructed in ArcMap to measure habitat use measures did not line up perfectly with the spot-mapping grid due to deviations in the 30.5 m distance between many grid points. Consequently, nine grid cells contained no sampled spot-mapping grid points and another nine contained two. However, the grid point associated with each grid cell was the closest to the cell center in all but three instances, and in each of these cases the corresponding grid point was within 3.8 meters of being the closest point. Therefore, I made the assumption that each grid point best represented its corresponding grid cell and assigned habitat, occupancy, and success rate values to the same sampling unit for regression analyses.

In separate analyses, I modeled occupancy and success rates using generalized linear models in R (R Development Core Team 2008). I assumed occupancy models to have a Poisson error distribution and success rates to have a binomial error distribution. For success rate models, I treated each occasion a bird with known reproductive status occupied a cell as a trial and coded the response as an $n \times 2$ matrix, where n was the total number of grid cells and the two columns were the number of successes and the number of failures, respectively (Presnell 2000). A repeated measures approach would have been most appropriate considering I calculated both response variables by aggregating data over the study period; however, I needed habitat measurements from every season to perform such an analysis. Thus, I committed "sacrificial pseudoreplication" (Hurlbert 1984: p. 205) by modeling occupancy and success rates. Because I only had habitat measures from one season, I made the assumption that the forest structure did not change considerably over the study period, which was reasonable considering that the study sites had not been subject to drastic anthropogenic or natural disturbance over the last century.

I fit seven candidate models based on past studies of Ovenbird habitat associations and experience observing Ovenbird behavior (Table 1). Because of structural differences between the study sites, I used an analysis of covariance (ANCOVA) design to estimate parameters for each variable for each site (Kutner et al. 2005). I used an Information Theoretic approach (Burnham and Anderson 1998) to determine weight of evidence for each model based on Akaike Information Criteria (AIC, Akaike 1973). All predictor variables were centered dividing by respective grand means. Binned residual plots indicated adequate model fit and Cook's distances did not indicate any influential observations (Gelman and Hill 2007). Overdispersion was assessed using a quasibinomial distribution and standard errors were corrected based on the estimated overdispersion parameter (Gelman and Hill 2007).

Positive spatial autocorrelation was predicted *a priori* for both the response and predictor variables because grid cells were smaller than Ovenbird territories and grid points (sampling unit for habitat variables) were relatively close and covered the study areas almost uniformly. Spatial autocorrelation among observations violates the assumption of independence and can cause parameter estimates to be unstable and imprecise. Moran's I indices (Table 2) based on 999 Monte Carlo simulations in GeoDa^{TM} (GeoDa Center for Geospatial Analysis and Computation, Arizona State University, Tempe, AZ) indicated the response and predictor variables used in the candidate models were spatially autocorrelated and variograms fit using residuals from the candidate models further confirmed lack of independence among observations.

I accounted for spatial autocorrelation using WinBUGS^{TM} (version 1.4.3, MRC Biostatistics Unit, Cambridge, UK) to fit a Conditional Autoregressive (CAR) Bayesian model complementary to the best model from the candidate set. CAR models include a spatial component composed of adjacency and weights matrices, which I constructed using second-order Queen contiguity in GeoDa. Bayesian statistical methods use prior information (when available) and collected data to produce a model with a posterior estimate; however, when an uninformative prior distribution is used, parameter estimates are nearly identical to those produced using frequentist statistical methods. I ran 10,000 iterations to reach convergence and based parameter estimates on an additional 30,000 iterations. I assessed model fit performing a linear regression between the fitted and observed occupancy values and success rates for each site.

Fidelity measures

I assessed site fidelity by calculating apparent return rates of banded birds following their first year on each site. I considered a bird to have returned if researchers resighted it the year after banding, regardless of whether its new territory was located within site boundaries or the number of times observed. This measure is termed an apparent return rate (Marshall et al. 2000) because I did not adjust it based on a resighting probability using an extension of the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) approach. However, birds that were alive and returned to the study area were unlikely to escape detection because researchers surveyed three territory widths (150-200 m) outside of the study sites several times during each season. Therefore, birds that failed to return either died or dispersed long distances. I tested for a relationship between first-year reproductive success and return rates using chi-square tests of independence (Sokal and Rohlf 1995). I excluded birds from analysis if they were banded prior to 1998 (5 OH, 0 RR) or during the last year of the study (1 OH, 2 RR).

I assessed territory fidelity by estimating shift distance and the proportion of territory overlap between territories. I calculated a territory center for each bird territory by averaging the coordinates of each location and drew territories using Hawth's Tools to create minimum convex polygons based on the locations (Fig. 2). I measured shift distance as the distance (m) between territory centers and proportional overlap as the proportion of the year t territory intersected by the year $t + 1$ territory. I did not measure shift distance or territory overlap when territories were located outside of the study sites. I excluded from analysis territories with fewer than three locations because a minimum convex polygon could not be drawn. Because number of locations was a significant predictor of territory size ($R^2 = 0.36$, $F = 211.6$, $df = 1, 381$, $P < 0.001$), territory overlap may have been prone to error because of detectability differences among

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individuals. Therefore, I considered shift distance to be a more reliable measure of territory fidelity when making inferences.

I used only first-year shifts to test the hypothesis that successful birds would have higher rates of territory fidelity than unsuccessful birds to avoid resampling individuals; however, resampling birds was unavoidable when testing whether older birds were more faithful to previous territories than younger birds. I tested both hypotheses using separate two-way mixed model analyses of variance (ANOVA) including a random site factor to account for possible violations of the assumption of independence raised by correlation of variances among observations within each site. I assessed the significance of the fixed effect of interest (reproductive success or age) using a likelihood ratio test comparing a full model that included the fixed effect of interest in addition to a fixed intercept and random site effect to a nested reduced model that excluded the fixed effect of interest (Bolker et al. 2008). I used maximum likelihood (ML) estimation for both models. Territory overlap was arcsine transformed (arcsine√overlap) to meet assumptions of normality. Diagnostic plots and Levene's tests for homogeneity indicated the residuals approximately met the assumptions of normality and homoscedasticity. Bird age, which was determined initially during banding, was compared among five age classes. SY birds returning for their first breeding season were considered one-year-olds and placed in the first age class; whereas birds banded as ASY birds were considered two-year-olds. Birds advanced to a new age class every year; however, I grouped all birds that lived five years or more into the fifth age class.

I quantified the degree of lifetime territorial consistency using similar measures of shift distance and territory overlap; however, instead of relating each movement to a bird's previous-year territory, I related all shifts to the first-year territory. Thus, I calculated the distance

between the first-year territory center and the center of every later territory during the period a bird returned. I measured overlap similarly as the proportion of the first-year territory that intersected territories from each return year. Because few birds ($n = 9$) lived beyond three years at RR, I combined data from both sites. Considering the proximity of bird territories that is apparent from maps of consecutive years (Fig. 3), I expected that measures of consistency would be similar among all years that birds returned. Finally, I performed a simulation using 1,000 birds shifting in random directions (0-359 degrees) each year over six years (five shifts). I randomly assigned shift distances from one year to the next using a bootstrapping approach (Efron and Tibshirani 1993) to resample between-year shift distances observed on the study sites. I created equal-sized circular territory polygons around each location using the mean territory diameter observed (67.6 m). For each year, I found the distance to the first-year territory using trigonometric functions and proportional overlap using the intersect tool in ArcMap. I made qualitative comparisons between the simulated pattern of territorial consistency and the observed pattern. I analyzed all fidelity data using R.

RESULTS

Habitat measures

At the site-level, mean density was 1.1 (SD = 0.2) males/ha at OH and 0.7 (0.1) males/ha at RR averaged among years (Fig. 4A). Mean reproductive success was 0.74 (SD = 0.11) at OH and 0.75 (SD = 0.11) at RR (Fig. 4B). However, reproductive success rates were 0.65 (SD = 0.16) and 0.61 (SD = 0.19) at each respective site when unknown birds (33 OH, 24 RR) were classified as unsuccessful.

Occupancy values of grid cells ranged from 0 to 15 with a mean of 6.3 bird-years at OH; whereas values ranged from 0 to 12 with a mean of 4.2 at RR (Fig. 5). Occupancy (Fig. 6A) and success rates (Fig. 6B) had a clustered pattern, which further supported the prediction that values would be positively autocorrelated in space. Success rates were not correlated with occupancy at either site (OH: $r = 0.08$, $df = 230$, $P = 0.21$; RR: $r = 0.12$, $df = 185$, $P = 0.11$) and were high at all levels of occupancy (Fig. 7A) with overall means of 0.75 (SD = 0.19) and 0.72 (SD = 0.27) at OH and RR, respectively. Only 5.6% (13/232) of cells at OH and 9.6% (18/187) of cells at RR had success rates lower than 0.50. Birds residing on high occupancy cells tended to be older than birds on low occupancy cells (Fig. 7B), which was a direct result of longer residency times of individuals occupying these cells (Fig. 7C).

Despite observable differences in habitat structure between the study sites, measured habitat variables varied little within each site (Table 3). The Obstructions and Perch Sites with Quadratic Effects and Obstructions and Perch Sites models received virtually all of the support based on AIC weights for habitat models predicting occupancy (Table 4A). Parameter estimates (Table 4B) indicated that shrub density, small tree density, and snag density had a positive relationship with occupancy; whereas, there was a negative relationship between rock cover and occupancy. However, shrub density at OH, rock cover at RR, and small tree density at both sites were the only significant effects based on 95% credible intervals from the CAR Bayesian model. The model explained 24.6% of the deviance and the linear regression between the fitted and observed values (Fitted occupancy = 2.90 + 0.47 * observed occupancy, $R^2 = 0.60$) indicated that the model was able to differentiate between the lowest (≤ 2 bird-years, 20.3% of cells) and highest (≥ 10 bird-years, 8.7% of cells) occupancy grid cells (Fig. 8A).

The Collins et al. 1982 model had the most support of the habitat models predicting success rates; however, four other models, included the intercept only model, had AIC weights greater than 0.10 (Table 5A). Excluding the intercept model, the four best models included shrub density and three included ground cover and canopy cover. Canopy cover at OH was the only significant effect based on 95% credible intervals from the Collins et al. 1982 CAR Bayesian model (Table 5B). The model explained 3.9% of the deviance and provided poor predictions of success rates (Fig. 8B) based on the linear regression between the fitted and observed values (Fitted success rate = 0.66 + 0.12 * observed success rate, $R^2 = 0.22$).

Fidelity measures

The majority of birds banded at OH (61/71) and RR (36/46) during the study period were second-year birds returning for their first season of breeding. Return rates following the first year were high (Table 6) and independent of past reproductive success (OH: $\chi^2 = 1.26$, $df = 1$, $p = 0.26$; RR: $\chi^2 = 0.07$, $df = 1$, $P = 0.78$). Similar results were observed when treating all birds with unknown reproductive status as unsuccessful (OH: $\chi^2 = 2.44$, $df = 1$, $p = 0.12$; RR: $\chi^2 = 0.36$, $df = 1$, $P = 0.55$). Birds frequently returned to the study sites beyond one year (Table 7); mean number of years returned was 3.3 years at OH and 2.3 years at RR.

I used 44 OH and 24 RR birds to analyze shift distances and territory overlap because seven birds that returned to each site had territories outside of the study sites. Averaging within each site, mean shift distance and territory overlap were 41.6 m (SD = 36.1 m) and 0.373 (SD = 0.288) at OH and 76.5 m (SD = 55.6 m) and 0.180 (SD = 0.212) at RR. Successful birds did not shift shorter distances than unsuccessful birds (Fig. 9A; $\chi^2 = 0.07$, $df = 1$, $P = 0.79$) or have higher territory overlap values (Fig. 9B; $\chi^2 = 0.07$, $df = 1$, $P = 0.80$). Similar results were

observed when treating all birds with unknown reproductive status as unsuccessful (Shifts: χ^2 = 0.06, df = 1, p = 0.81; Overlap: χ^2 = 0.45, df = 1, p = 0.50). Shift distance differed among age classes (χ^2 = 14.9, df = 4, $P < 0.01$); first-year shifts tended to be farther than shifts in later years (Fig. 10A). Territory overlap (Fig. 10B) did not differ among age classes (χ^2 = 4.4, df = 4, P = 0.36).

Using all second-year and later territories (n = 203), birds moved a mean distance of 65.5 m (SD = 51.1) from their first-year territory during their lifetime on each site; mean overlap with the first-year territory was 0.239 (SD = 0.266). Assuming the average territory (area = 0.36-ha) to be in the shape of a circle, the mean distance shifted was approximately equivalent to the diameter (67.6 m) of one territory (one territory width). Thirty-seven lifetime shifts were beyond 100 m, the longest being 302.8 m or 4.5 territory widths. There was a trend for the distance from the first-year territory to increase and first-year overlap to decrease each year birds returned to the sites (Fig. 11), indicating that despite high rates of territory fidelity during consecutive years, territories tended to drift apart. Territory maps did not indicate that birds moved away from their first-year territory in a constant direction, and the simulation shifting birds in random directions produced results that were nearly identical to those observed (Fig. 11).

DISCUSSION

The high rates of reproductive success and returns observed in the present investigation were in accordance with past studies conducted at OH and RR and other locations, which found Ovenbirds to occur and succeed at high rates in large tracts of mature, deciduous forest (Porneluzi et al. 1993, Villard et al. 1993, Burke and Nol 1998, Porneluzi and Faaborg 1999,

Bayne and Hobson 2001). Although reproductive success rates within grid cells varied somewhat over both study sites, the vast majority of cells (over 90%) had success rates greater than 0.50, indicating that habitat quality was relatively homogenous at the territory scale as males had a high probability of reproducing from nearly every location on site. Considering that researchers have found birds in heterogeneous habitats to move to better territories when they become available (Krebs 1971, Beletsky and Orians 1987), the observed lack of dispersal on the study sites and the low level of variation among measured habitat variables further supported this inference.

Occupancy varied considerably throughout both study sites, but it was not correlated with success rates as predicted. Instead, individual differences in lifespan strongly influenced occupancy scores as the grid cells with the highest scores often were part of the territories of the longest-lived birds on each site because birds moved little between years. These birds may have had traits that allowed them to survive longer than most of the population, but success rates of grid cells they occupied did not differ from other locations on the study sites occupied by shorter-lived birds. Differences in bird quality may explain differences in lifespan or even lifetime productivity, but long-lived birds did not receive an advantage from the territories they occupied. The lack of a correlation between occupancy and success rates using the present scale of analysis reaffirms Johnson's (2007) recommendation that researchers estimate habitat quality using demographic measurements because surrogates may be misleading indicators.

The poor fit of habitat selection models explaining success rates likely resulted from low variation of both the predictor and response variables. Interestingly, the Obstructions and Perch Sites with Quadratic Effects model performed well when differentiating between the highest and lowest occupancy grid cells on the study sites. Occupancy tended to be higher in areas with low

rock cover and high densities of both shrubs and small (<23 cm DBH) trees. If the apparent preference for these habitat features reflected areas most suitable for Ovenbird life history needs, then less favorable grid cells likely were "rescued" by higher quality cells in the same territory because reproductive success did not decline at the lowest occupancy grid cells. The habitat relationships I observed likely were site-specific because they departed from past studies that have found Ovenbird use to be associated with low ground cover and large (> 23 cm DBH) trees (Smith 1977, Collins et al. 1982, Smith and Shugart 1987, Wenny et al. 1993).

Researchers believe a proportion of birds that fail to return between breeding seasons are alive, but have dispersed away from study areas (Greenwood 1980, Greenwood and Harvey 1982, Marshall et al. 2000). Declines in return rates following experimentally-induced breeding failure provide compelling evidence that birds may consider prior breeding performance when deciding whether to reuse a site (Bollinger and Gavin 1989, Haas 1998, Hoover 2003). There was no evidence of such a trend for Ovenbirds in the present investigation. Birds returned to the study sites at high rates regardless of reproductive success and they rarely moved more than a territory width during their lifetime. Because birds never moved between the study sites (approximately 1.5 km) over the 21-year banding period (Goodrich unpubl. data) and few were banded as after second-year birds, it is likely that the small movements observed provided a true representation of breeding dispersal for this population.

Switzer (1993) modeled site fidelity and found that the "always stay" strategy performed better than the "win-stay: lose-switch" strategy for individuals occupying unpredictable habitats with little variation in quality among territories. Although habitat quality was high throughout OH and RR, reproductive failure was unpredictable because it was not autocorrelated in time or space during the study period. The biggest source of failure was likely predation because

researchers occasionally found nests destroyed (Goodrich pers. obs); whereas, rates of brood parasitism by Brown-headed Cowbirds (*Molothus ater*) were low (i.e. there were two cases during my three field seasons). Hoover et al. (1995) previously determined that the predator community at OH and RR consisted of a variety of birds, snakes, and mammals, and other investigators have found nest predation to be unpredictable in predator-rich systems (Filliater et al. 1994, Wilson and Cooper 1998).

In his study of Prothonotary Warblers in Illinois, Hoover (2003) reported that territory quality was predictable and heterogeneous at his study sites because the number of broods (0-2) produced varied among territories, but was consistent between years within a territory. Furthermore, nearly all untreated sites used in studies that manipulated reproductive success had lower success rates (56%, Bollinger and Gavin 1989; 36% and 46%, Haas 1998; 40%, Hoover 2003) than conservative estimates in this investigation (61-65%). The lone exception was the high quality site used by Bollinger and Gavin (1989), where success rates (70%) were nearly identical to OH (74%) and RR (75%) and return rates and local dispersal did not differ based on past performance. The patterns observed in these examples lend support to Switzer's (1993) contention that birds may use different decision rules depending on their habitat, adopting a strategy of unconditionally maintaining residency on homogeneous, high quality habitats or basing dispersal decisions upon reproductive performance in low quality or highly heterogeneous habitats.

In addition to assessing the quality of their own territories, birds would need to make broad assessments of neighboring areas to determine which strategy is most appropriate. Interestingly, Bollinger and Gavin (1989) reported that return rates were more highly correlated with overall site productivity than any other reproductive measure; whereas, Hoover (2003)

noted a tendency for unsuccessful birds to reuse the same territory if their neighbors had bred successfully. Both authors proposed that birds may consider the performance of their neighbors in addition to personal experience when deciding whether to reuse a breeding site. In fact, Hoover (2003) emphasized that monitoring neighbors may be more selfishly-motivated if extrapair copulations are common with neighboring females. This mechanism could explain patterns of site fidelity at OH and RR because birds were likely to have several successful neighbors. However, alternative hypotheses, such as population pressure (Weatherhead and Boak 1986) or monitoring of resources (Smith and Shugart 1987), cannot be eliminated based on the results from the present study.

Birds tended to shift farther distances following their first year than in later years; however, nearly all between-year shifts were less than a territory-width. Other studies have found site fidelity to increase with age (Greenwood and Harvey 1982, Harvey et al. 1984, Montalvo and Potti 1992, Payne and Payne 1993, Newton 2001). Researchers hypothesize that familiarity with a site may promote increasing philopatry by allowing more efficient use of resources and providing advantages that make territory defense easier. Furthermore, social dominance increases with age in some species (Smith et al. 1980, Rohwer et al. 1981, Sherry and Holmes 1989, Sergio et al. 2009), which also may aid in territory defense. Payne and Payne (1993) even suggested that familiarity with neighbors may encourage birds to reuse former territories because establishing relationships with a new set of neighbors may be more costly in terms of time and energy. Future studies addressing social interactions and aggressive encounters likely would be necessary to gain a better understanding of the factors contributing to this pattern.

Although birds moved little between years and placed their territories in similar locations, they tended to move farther away from their first breeding territory each year they returned. I may have predicted shifts to follow a directional pattern if there was a clear quality gradient on the study sites (e.g. transition from forest edge to core), but success rates were generally high at all locations. Furthermore, territory maps suggested that shifts did not follow a consistent direction, and the simulation that shifted birds in random directions produced a nearly identical "territory drift" pattern. These findings may further support the notion that quality was relatively homogenous over the study sites because there were no penalties to reproductive performance if birds did not return to the exact location of their previous territories.

The results of this investigation depart from other studies which have found a relationship between breeding dispersal and past reproductive success, and the lack of territory movements of Ovenbirds at Hawk Mountain Sanctuary may represent a general case for songbirds breeding in stable, high quality habitats, where sources of failure are infrequent and unpredictable. Birds may base dispersal decisions on more than personal breeding experience by monitoring the performance of neighbors to make broader assessments of habitat quality. Experiments manipulating breeding success of adjacent pairs would test for the possibility of neighborhood effects. The "territory drift" pattern observed over the lifetime of Ovenbirds warrants inquiry into whether other long-term studies found similar results. Further consideration of the mechanisms producing this pattern and their biological significance may be necessary.

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Table 1. Models used in regression analyses to predict Ovenbird occupancy and reproductive success patterns at Owl's Head and River of Rocks sites during the study period from 1998 to 2009. Models were based on previous studies and experience observing Ovenbirds. Parameters, including intercept terms, were estimated for each site separately using an ANCOVA design.

Model	Habitat Variables	Parameters estimated
Intercept	None	2
Smith 1977[a]	Canopy cover + canopy height - ground cover - shrub density + small tree density + large tree density	14
Collins et al. 1982[a]	Canopy cover - ground cover - shrub density	8
Smith and Shugart 1987[a]	Canopy cover - conifer density - ground cover - shrub density + small tree density + large tree density	14
Robbins et al. 1989[a]	Canopy height - slope + small tree density + large tree density	10
Wenny et al. 1993[a]	Canopy cover - ground cover + litter depth - shrub density - snag density + small tree density + large tree density	16
Nesting and Feeding Obstructions[b]	-Rock cover - shrub density	6
Obstructions and Perch Sites[c]	-Rock cover - shrub density + small tree density + snag density	10
Obstructions and Perch Sites with Quadratic Effects[d]	-Rock cover - shrub density + small tree density + snag density + rock cover^2 + shrub density^2 - small tree density^2	16

[a]Studies cited were primary ones whose findings were used to construct similar habitat models based on the variables I collected.

[b]Model based on experience observing Ovenbird behavior and hypothesis that the dominant ground cover types (shrubs and rocks) limit space available for foraging and nesting.

[c]Model that builds on Nesting and Feeding Obstructions model based on experience observing Ovenbirds using smaller trees (<23 cm DBH) and snags as perch sites.

[d]Model that builds on Obstructions and Perch Sites by assuming nonlinear relationship between dependent variables and rock cover, shrub density, and small tree density.

Table 2. Moran's I and *P* values for response and predictor variables included in habitat selection models predicting Ovenbird occupancy and reproductive success patterns at Owl's Head and River of Rocks sites during the study period from 1998 to 2009. A second-order Queen's contiguity weights matrix was used to estimate Moran's I values and *P* values were calculated based on 999 randomizations of observed data.

Variable	Owl's Head		River of Rocks	
	Moran's I	*P*	Moran's I	*P*
Occupancy	0.222	0.001	0.300	0.001
Success rates	0.104	0.001	0.200	0.001
Canopy cover	0.102	0.002	0.154	0.001
Canopy height	0.078	0.003	0.098	0.001
Conifer density	-0.007	0.356	0.028	0.066
Ground cover	0.127	0.001	0.124	0.001
Large tree density	0.065	0.006	0.087	0.004
Litter depth	0.250	0.001	0.150	0.001
Rock cover	0.444	0.001	0.220	0.001
Shrub density	0.076	0.004	0.082	0.005
Slope	0.352	0.001	0.166	0.001
Small tree density	0.280	0.001	0.159	0.001
Snag density	0.096	0.001	0.141	0.001

Table 3. Means (SD) of habitat variables measured at Owl's Head ($n = 238$, 19.4 ha) and River of Rocks ($n = 210$, 16.9 ha) sites during summer of 2008.

Habitat variable	Site	
	OH	RR
Canopy cover (%)	87.6 (7.4)	87.7 (3.3)
Canopy height (m)	19.9 (4.5)	23.5 (3.7)
Cover (%)		
Bare	0.1 (0.9)	0.4 (1.7)
Fern (<50 cm height)	3.1 (12.0)	0.4 (2.3)
Forb (<50 cm height)	8.7 (7.8)	4.2 (4.4)
Green[a]	39.5 (27.6)	16.9 (12.7)
Litter	56.4 (27.0)	58.5 (21.3)
Log	2.1 (1.6)	2.1 (2.1)
Other[b]	1.3 (7.1)	0.3 (1.4)
Moss	1.6 (4.4)	1.8 (2.7)
Rock	2.1 (7.3)	22.5 (21.6)
Shrub (<50 cm height)	26.8 (22.4)	10.9 (9.9)
Litter depth (mm)	26.6 (6.3)	30.4 (11.0)
Tree density (stems per 100 m^2)		
Conifer	0.1 (0.9)	0.2 (0.4)
Large (>23 cm DBH)	2.5 (1.1)	2.6 (0.8)
Small (<23 cm DBH)	14.4 (5.6)	10.1 (3.6)
Snags	2.3 (1.2)	1.7 (1.0)
Shrub density (stems per 10 m^2)	16.7 (15.6)	9.7 (8.6)
Slope (degrees)	3.0 (1.5)	6.4 (2.5)

[a]Estimate of vegetative ground cover.
[b]Grass, water, marsh, and brush cover estimates combined.

Table 4. A. Model selection summary of habitat models predicting Ovenbird occupancy at Owl's Head and River of Rocks sites during study period from 1998 to 2009, where K is the number of parameters (including intercept term), Log(L) is the log likelihood, AIC is Akaike Information Criteria, Δ_i is the difference between the AIC value for each model and the model with the lowest AIC, and w_i is the AIC weight for each model.

Model	K	Log(L)	AIC	Δ_i	w_i
Obstructions and Perch Sites with Quadratic Effects	16	-1073.0	2178.0	0.0	0.66
Obstructions and Perch Sites	10	-1079.7	2179.3	1.3	0.34
Wenny et al. 1993	16	-1079.4	2188.9	10.9	<0.01
Nesting and Feeding Obstructions	6	-1090.4	2192.8	14.8	<0.01
Smith and Shugart 1987	14	-1087.3	2202.6	24.6	<0.01
Smith 1977	14	-1087.8	2203.6	25.6	<0.01
Collins et al. 1982	8	-1104.1	2224.2	46.2	<0.01
Robbins et al. 1989	10	-1124.5	2269.0	91	<0.01
Intercept	2	-1182.8	2367.6	189.6	<0.01

Table 4. B. Parameter estimates (SD) from Conditional Autoregressive (CAR) Bayesian model complementary to the Obstructions and Perch Sites with Quadratic Effects model of Ovenbird occupancy patterns at Owl's Head and River of Rocks sites during study period from 1998 to 2009. Asterisks indicate significant effects based on 95% credible intervals of parameter estimates.

Variable	Owl's Head	River of Rocks
Shrub density	0.149 (0.070)*	0.179 (0.144)
Rock cover	-0.064 (0.132)	-0.213 (0.069)*
Small tree density	0.572 (0.291)*	1.168 (0.607)*
Snag density	0.059 (0.051)	0.031 (0.083)
Shrub density^2	-0.030 (0.016)	-0.038 (0.047)
Rock cover^2	-0.011 (0.028)	0.013 (0.011)
Small tree density^2	-0.164 (0.107)	-0.519 (0.302)

Table 5. A. A. Model selection summary of habitat models predicting Ovenbird rates of reproductive success at Owl's Head and River of Rocks sites during study period from 1998 to 2009, where K is the number of parameters (including intercept term), Log(L) is the log likelihood, AIC is Akaike Information Criteria, Δ_i is the difference between the AIC value for each model and the model with the lowest AIC, and w_i is the AIC weight for each model.

Model	K	Log(L)	AIC	Δ_i	w_i
Collins et al. 1982	8	-502.8	1021.5	0.0	0.39
Intercept	2	-510.7	1023.5	2.0	0.15
Smith 1977	14	-497.7	1023.5	2.0	0.14
Nesting and Feeding Obstructions	6	-505.9	1023.8	2.3	0.12
Wenny et al. 1993	16	-497.1	1024.2	2.7	0.10
Smith and Shugart 1987	14	-498.6	1025.2	3.7	0.06
Robbins et al. 1989	10	-503.3	1026.6	5.1	0.03
Obstructions and Perch Sites	10	-504.8	1029.7	8.2	0.01
Obstructions and Perch Sites with Quadratic Effects	16	-502.1	1036.2	14.7	<0.01

Table 5. B. Parameter estimates (SD) from Conditional Autoregressive (CAR) Bayesian model complementary to the Collins et al. 1982 model of Ovenbird reproductive success patterns at Owl's Head and River of Rocks sites during study period from 1998 to 2009. Asterisks indicate significant effects based on 95% credible intervals of parameter estimates.

Variable	Owl's Head	River of Rocks
Canopy cover	-3.031 (1.572)*	-4.224 (2.159)
Ground cover	0.161 (0.114)	0.127 (0.282)
Shrub density	-0.076 (0.091)	-0.070 (0.176)

Table 6. Return rates of Ovenbirds banded between 1998 and 2008 at Owl's Head (OH) and River of Rocks (RR) study sites following their first year. Birds were grouped based on reproductive performance during the first year.

Bird Status	OH		RR	
	n	Proportion Returned	*n*	Proportion Returned
Successful	45	0.667	33	0.606
Unsuccessful	12	0.833	9	0.556
Unknown	13	0.846	12	0.500
Combined	70	0.729	54	0.574

Table 7. Distribution of the number of years banded Ovenbirds returned to Owl's Head (OH) and River of Rocks (RR) during 12 year study period, 1998-2009. Birds banded prior to 1998 (5 OH, 0 RR) or during the last year (1 OH, 2 RR) were not counted. Sixteen birds (14 OH, 2 RR) included were alive at the end of the 2009 season.

Years on site	Number of birds	
	OH	RR
1	19	23
2	12	12
3	14	10
4	7	3
5	8	3
6	3	1
7	2	2
8	2	0
9	2	0
10	0	0
11	1	0
Total	70	54
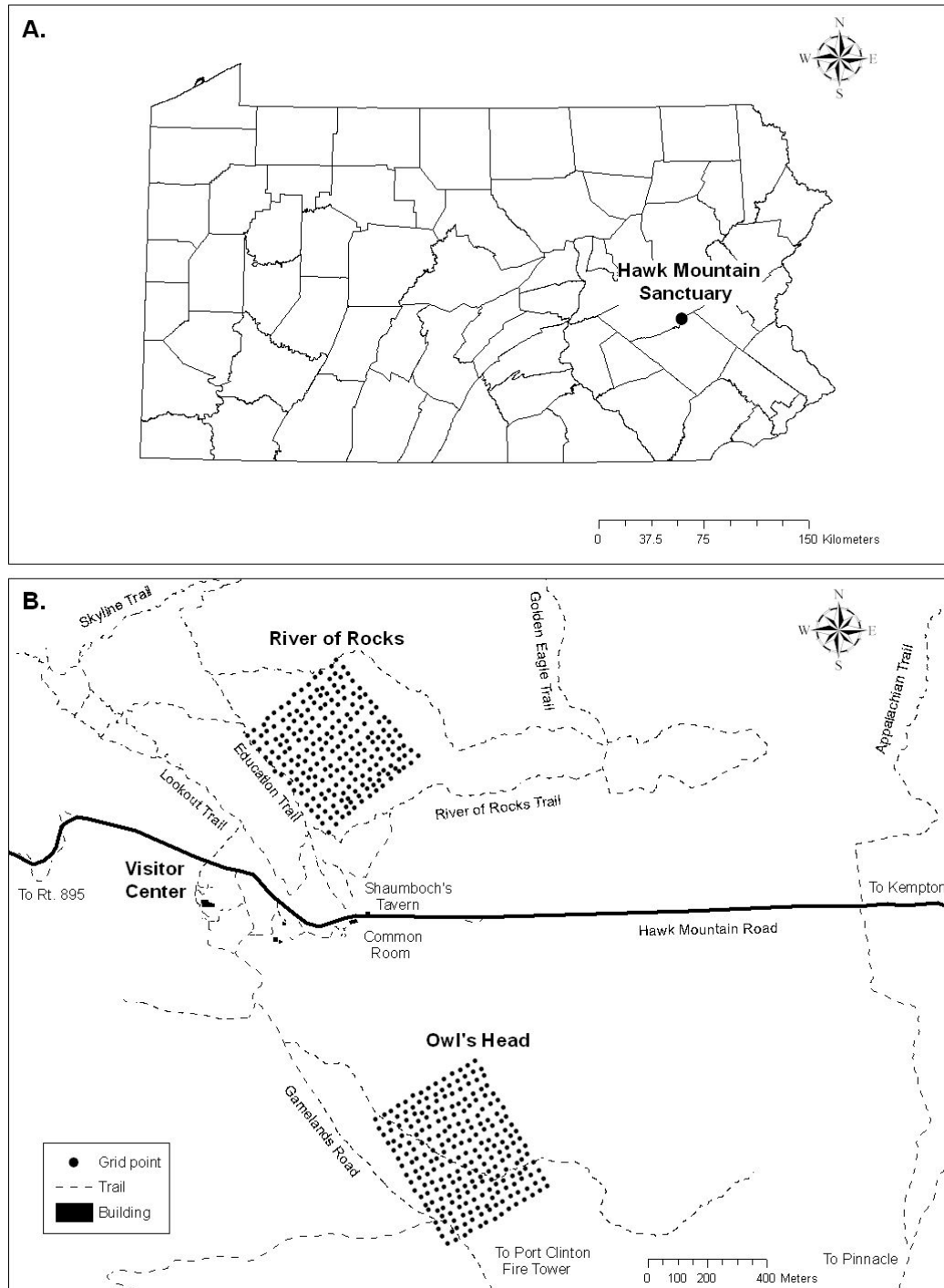
Fig. 1. A. Location of Hawk Mountain Sanctuary in eastern Pennsylvania. B. Owl's Head (OH) and River of Rocks (RR) study sites at Hawk Mountain Sanctuary. Grid points used for spot-mapping censuses are marked in the field by flagging tape and labeled alphanumerically.
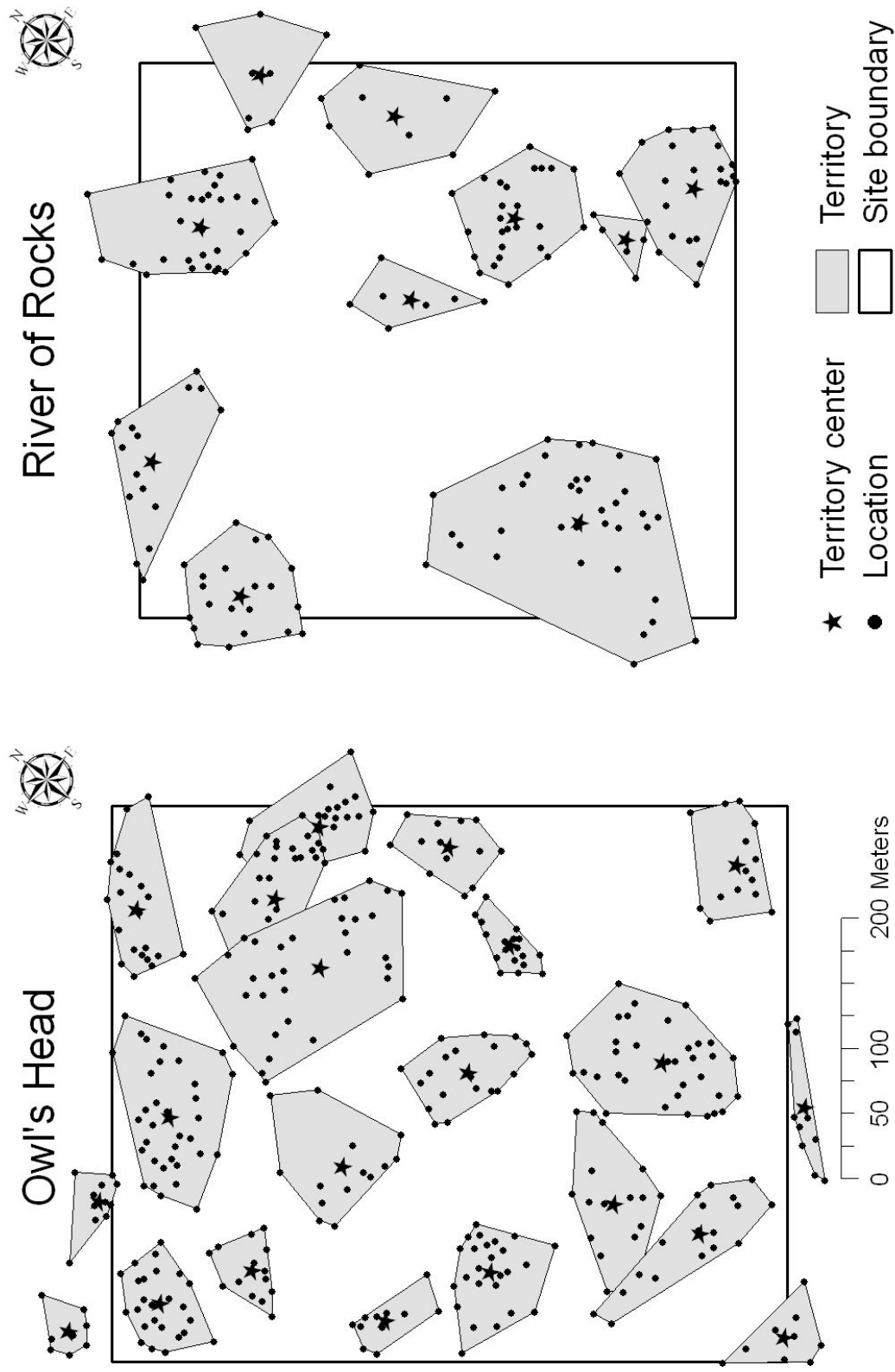
Fig. 2. Territory centers and minimum convex polygons based on spot-mapped locations of Ovenbirds using 2009 birds at Owl's Head and River of Rocks sites, Hawk Mountain Sanctuary.
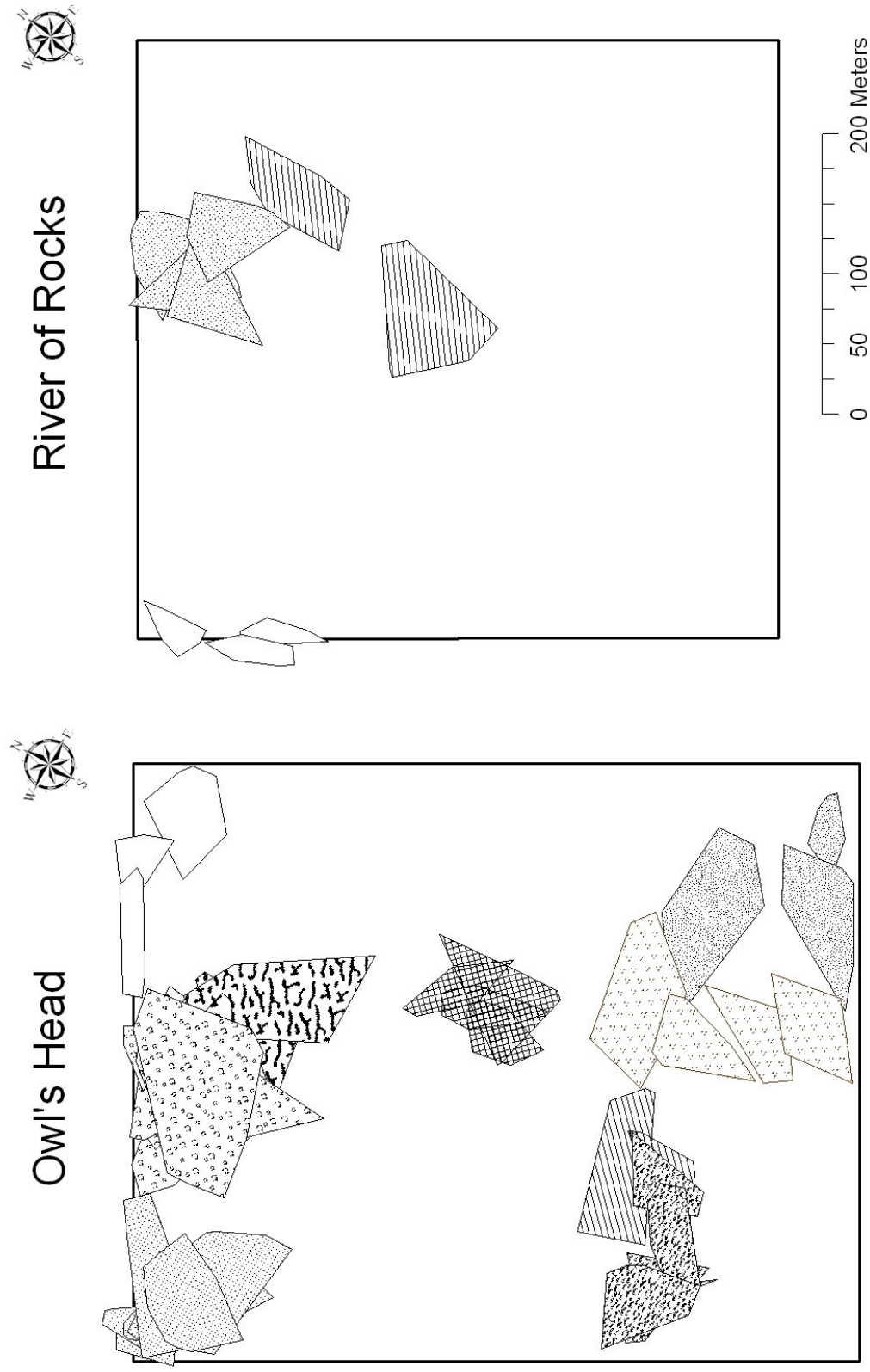
Fig. 3. Demonstration of typical year-to-year territory shifts using maps from each year birds banded in 2002 returned to Owl's Head and River of Rocks sites. Polygons of the same pattern represent territories occupied by the same bird during different years.

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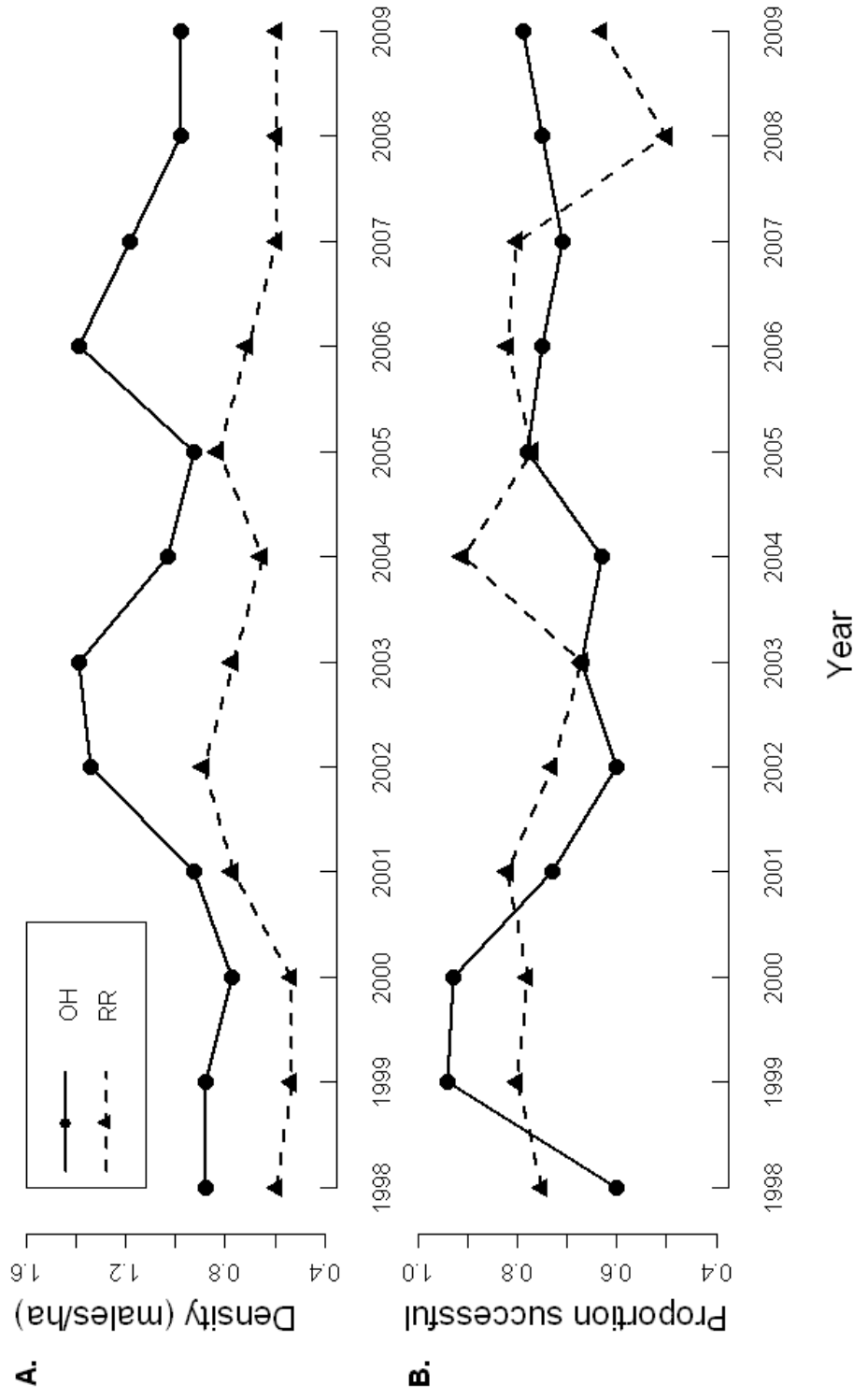
Fig. 4. A. Male density (males/ha) of Ovenbirds at Owl's Head (OH) and River of Rocks (RR) study sites. Males were included in density calculations if at least one spot-mapped location occurred within site boundaries. B. Proportion of males that bred successfully at OH and RR during 1998 to 2009.
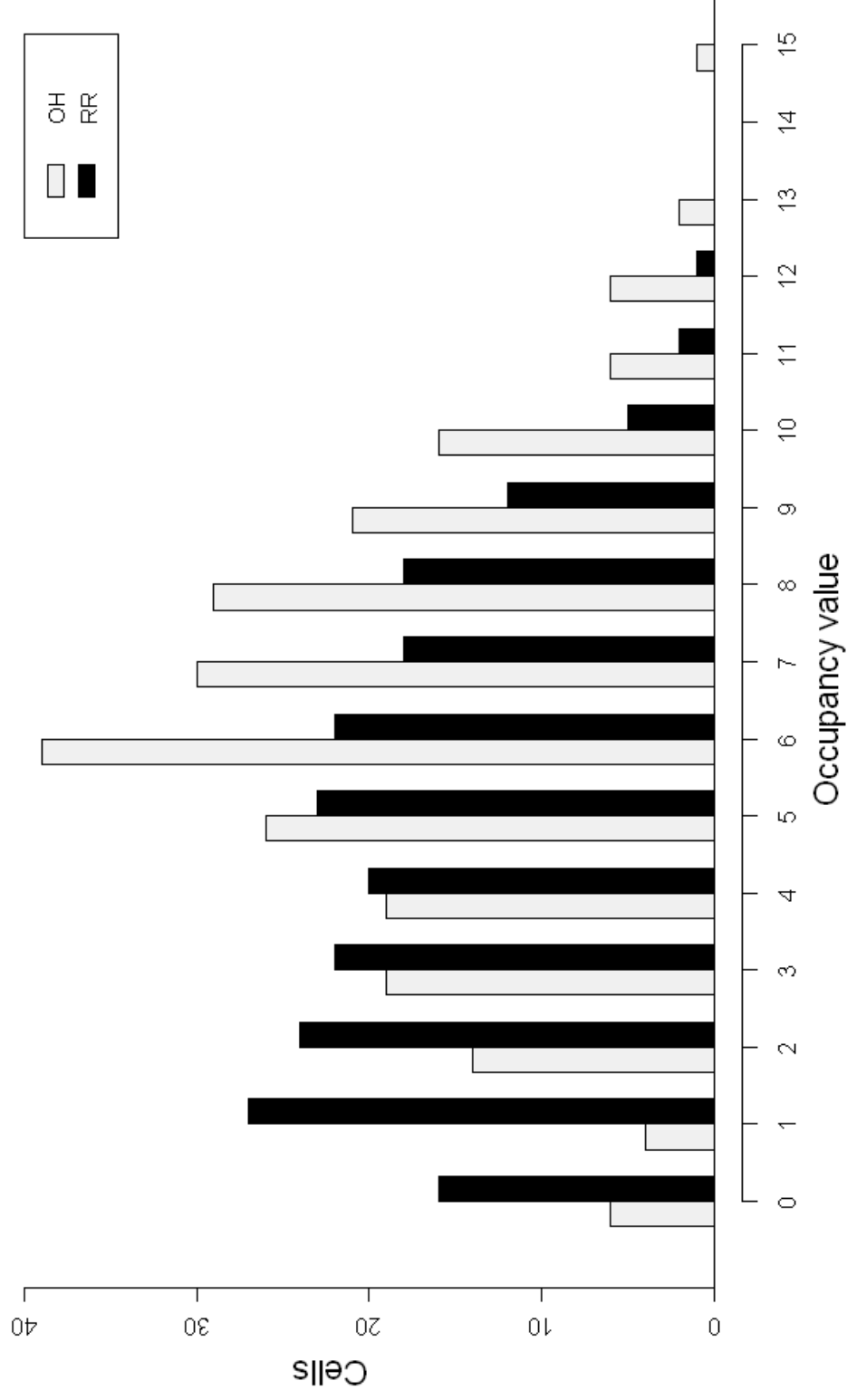
Fig. 5. Number of grid cells (30 m × 30 m) at each occupancy level (units = total bird-years) at Owl's Head (OH) and River of Rocks (RR) study sites over 12-year study period, 1998-2009.

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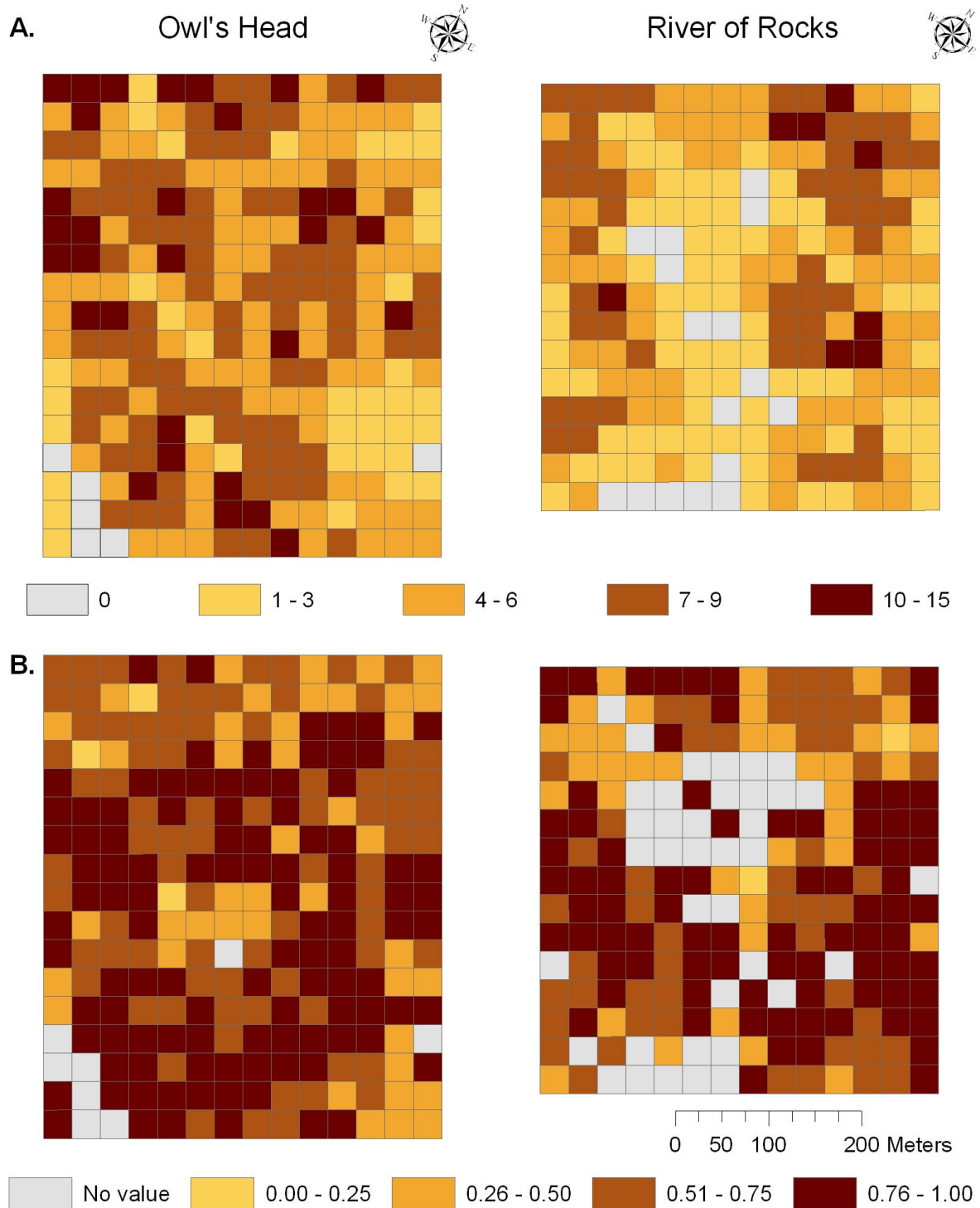
Fig. 6. A. Spatial variation of occupancy (units = total bird-years) at Owl's Head and River of Rocks sites over 12-year study period, 1998-2009. B. Spatial variation of reproductive success rates (proportion successful) at Owl's Head and River of Rocks sites over study period.
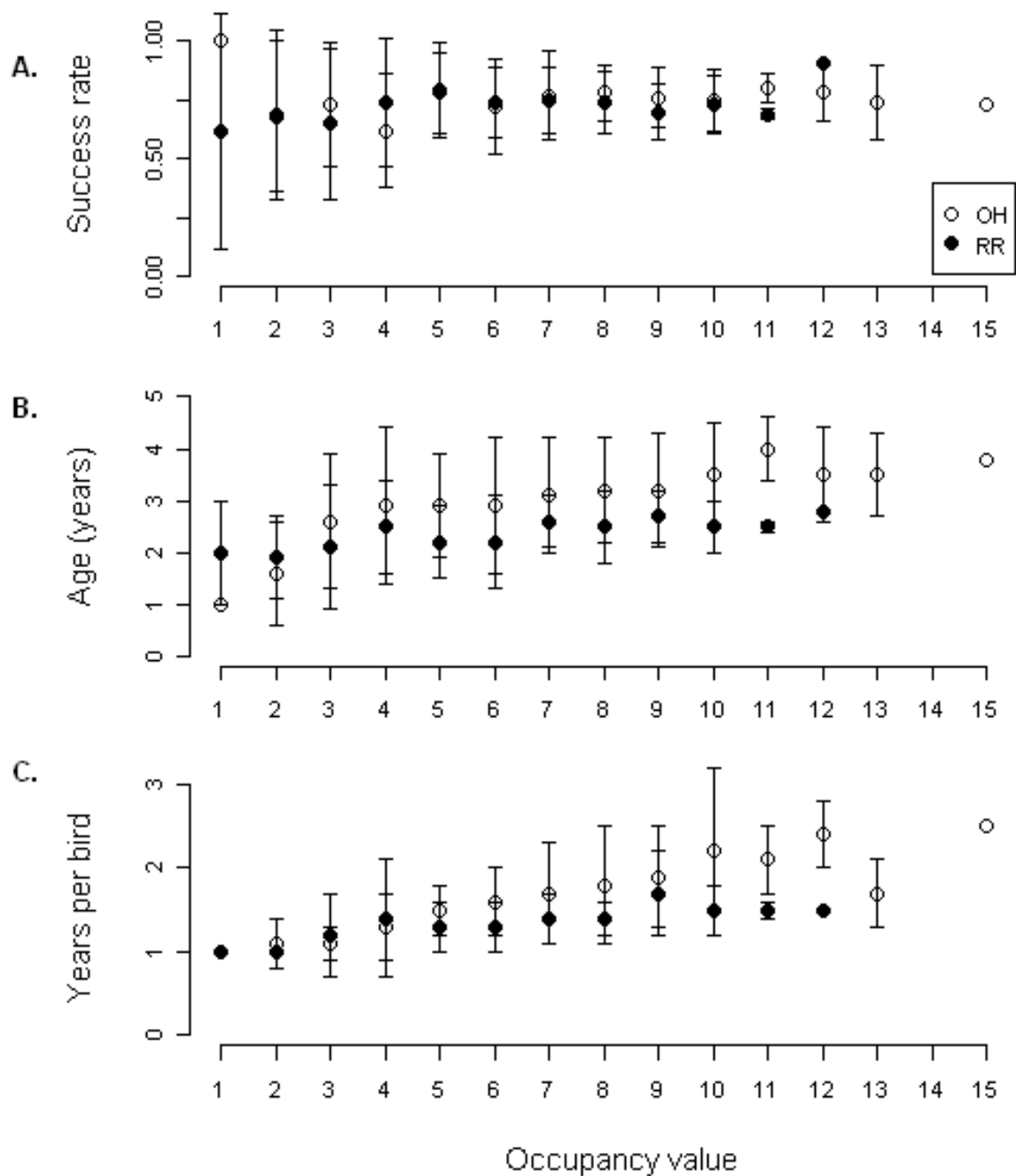
Fig. 7. A. Mean (± SD) success rates (proportion successful) of Ovenbirds in cells at each occupancy level (total bird-years) at Owl's Head (OH) and River of Rocks (RR) study sites during 12-year study period, 1998-2009. B. Mean (± SD) age (years) of birds at each occupancy level. C. Mean (± SD) number of years individuals occupied cells at each occupancy level.
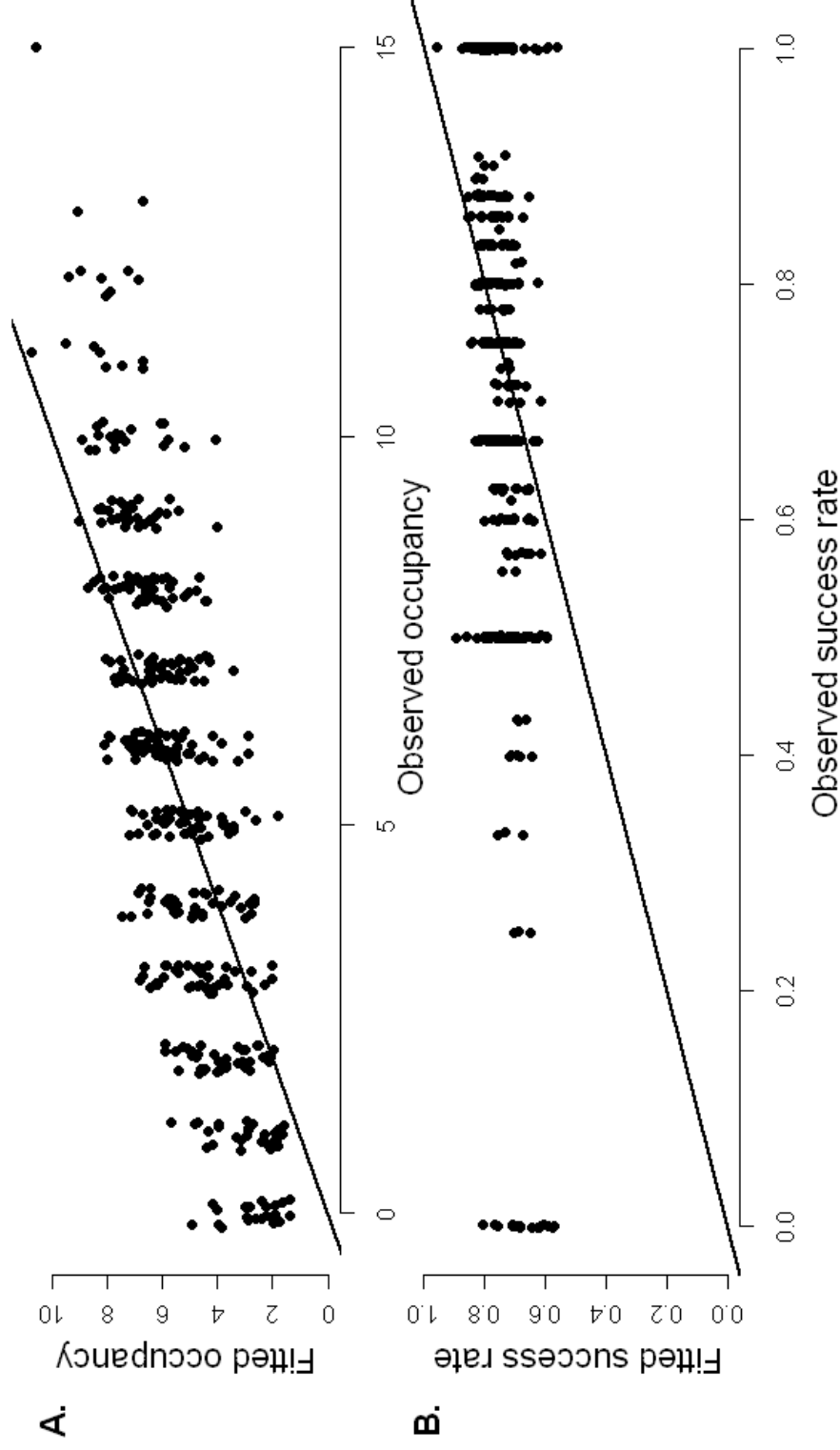
Fig. 8. A. Observed occupancy values versus fitted occupancy values from Obstructions and Perch Sites with Quadratic Effects conditional autoregressive (CAR) Bayesian model. B. Observed success rate values versus fitted success rate values from Collins et al. 1982 CAR Bayesian model. Plotted lines represent perfect fit with intercept of 0 and slope of 1.

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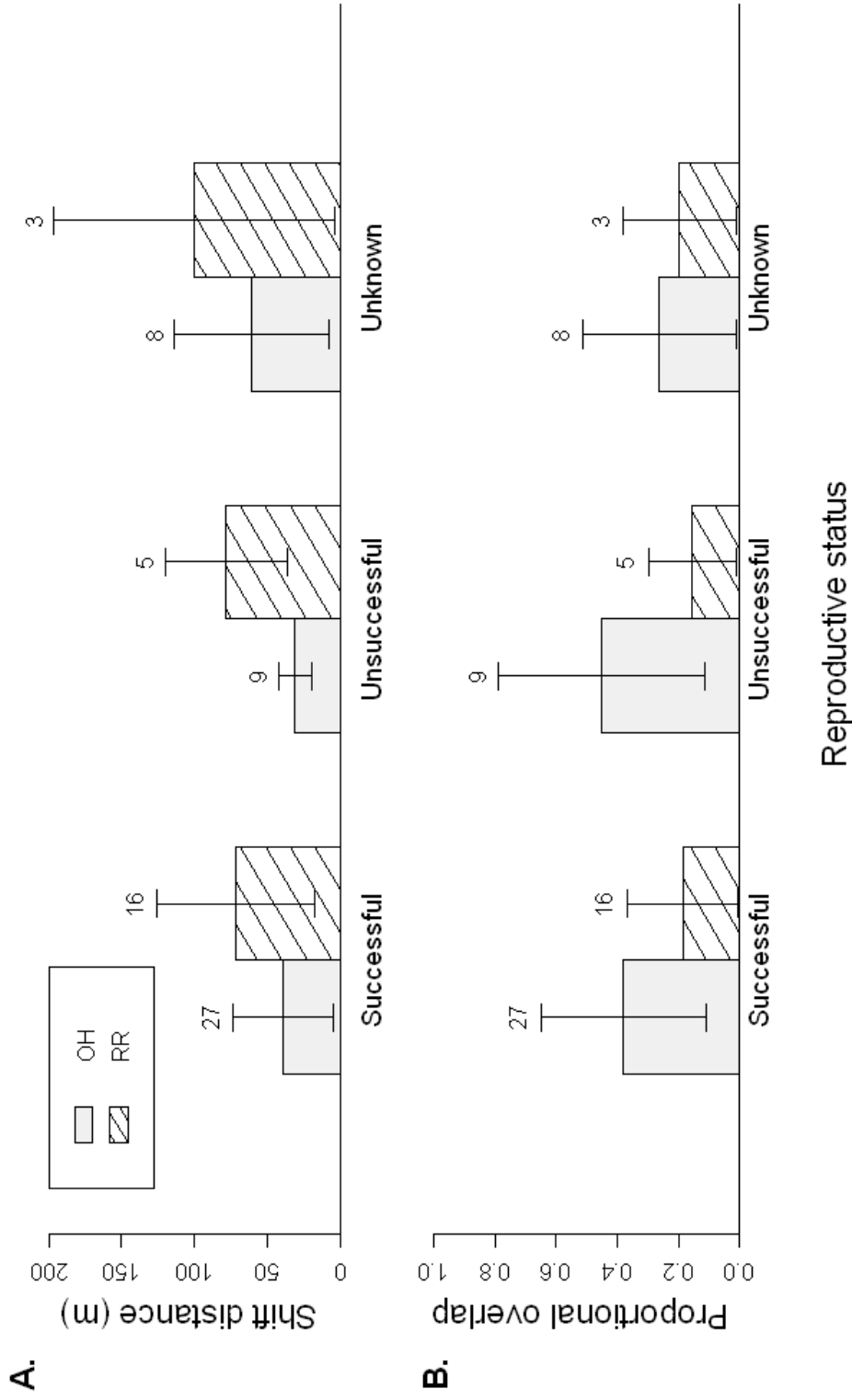
Fig. 9. A. Mean (± SD) shift distances (m) of Ovenbirds differing in reproductive status during their first year on Owl's Head (OH) and River of Rocks (RR) study sites during the 12-year study period, 1998-2009. B. Mean (± SD) proportional overlap of territories of birds differing in reproductive status during their first year at OH and RR during the study. Sample sizes indicated above bars.
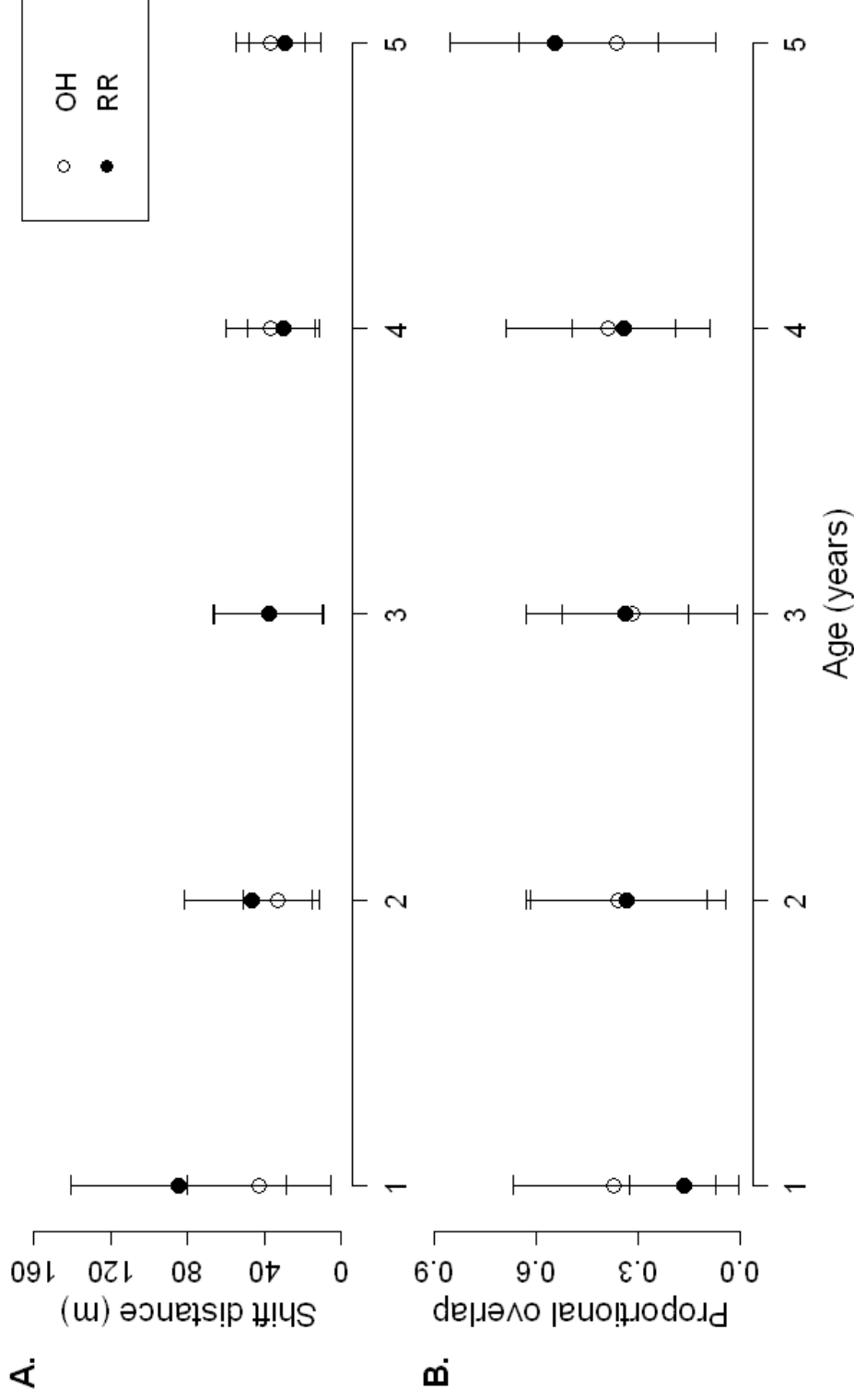
Fig. 10. A. Mean (± SD) shift distances (m) of Ovenbirds in different age classes at Owl's Head (OH) and River of Rocks (RR) sites during 12-year study period, 1998-2009. B. Mean (± SD) proportional overlap of territories of birds in different age classes at OH and RR during the study. Sample sizes in each respective age class were 40, 34, 22, 17, and 26 at OH and 20, 18, 13, 6, and 5 at RR.
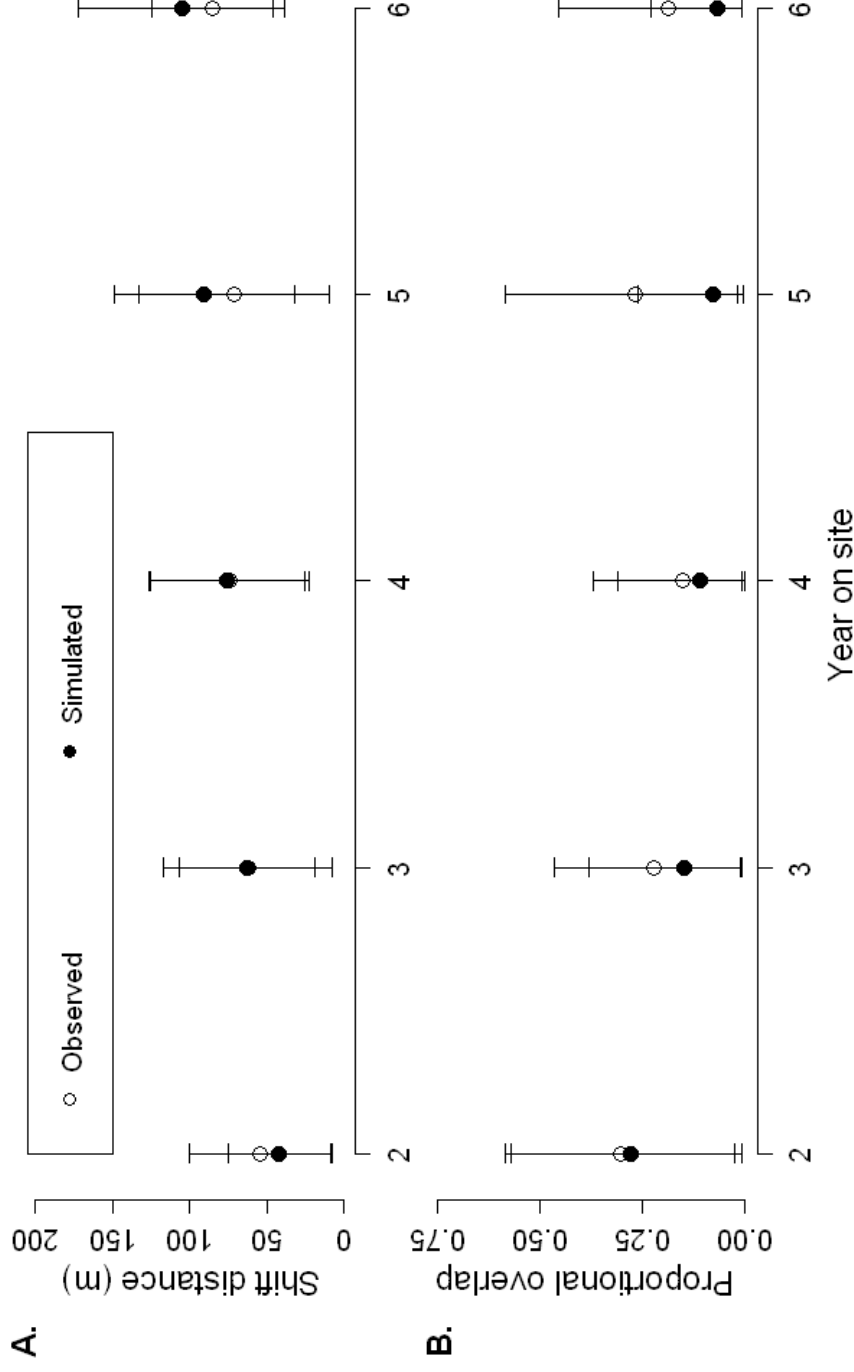
Fig. 11. A. Mean (±SD) distance (m) from first-year territory observed for each year Ovenbirds returned to study sites during 12-year study period, 1998-2009, and for returns simulated by assigning random shift directions each year using 1,000 birds. B. Mean (±SD) proportional overlap (m) with first-year territory for each year birds returned to study sites and for randomly simulated returns. Sixth-year and older territories were placed in the final grouping. Sample sizes in respective year groupings were 68, 51, 33, 22, and 29.

APPENDIX A

Study Site Habitat Maps

Spatial variation of canopy cover at Owl's Head and River of Rocks study sites.

River of Rocks

Owl's Head

0   50   100   200 Meters

Canopy cover (% covered)

0.0 - 75.0	75.1 - 80.0	80.1 - 85.0	85.1 - 90.0	90.1 - 95.0
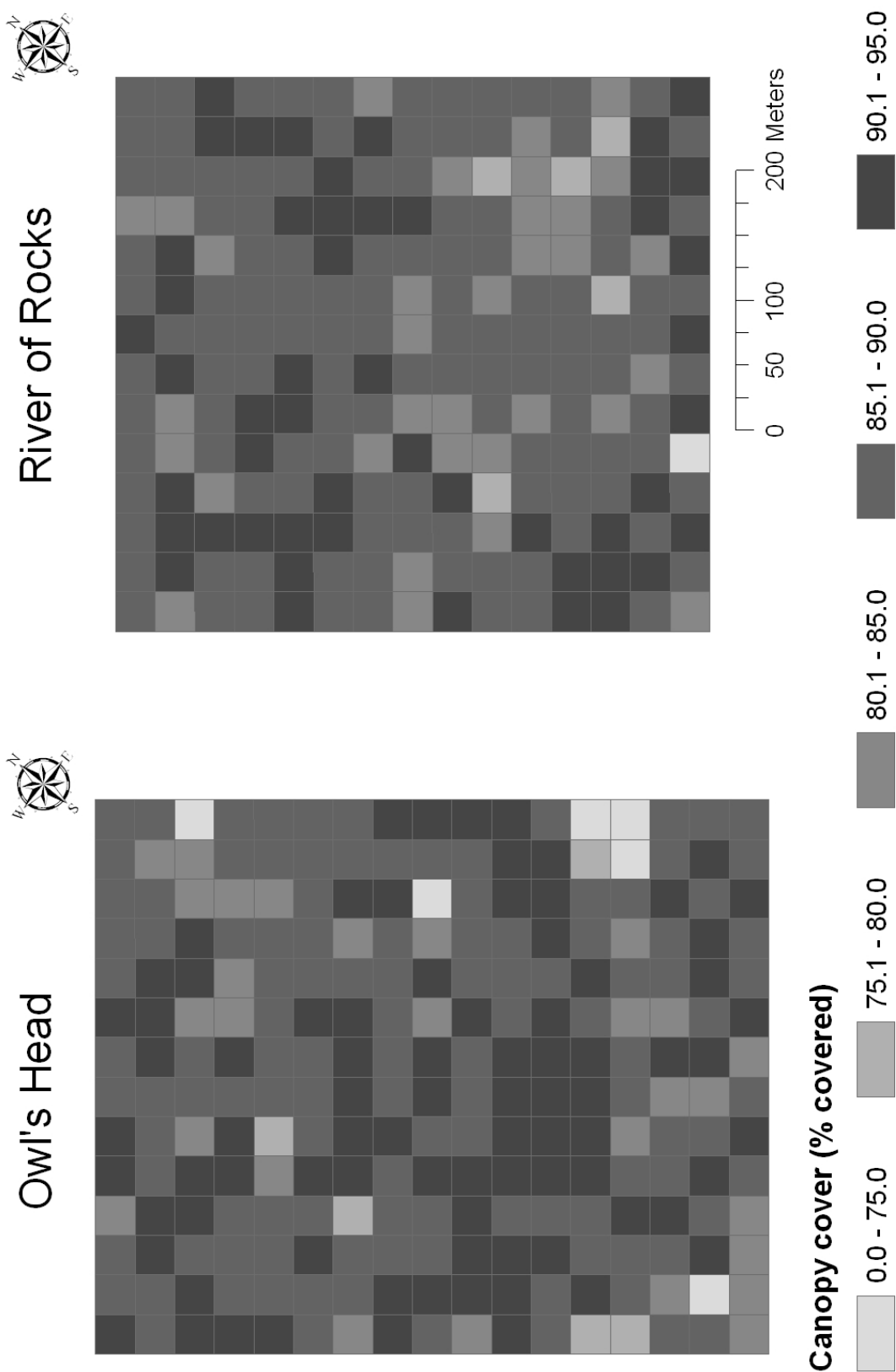
Spatial variation of canopy height at Owl's Head and River of Rocks study sites.

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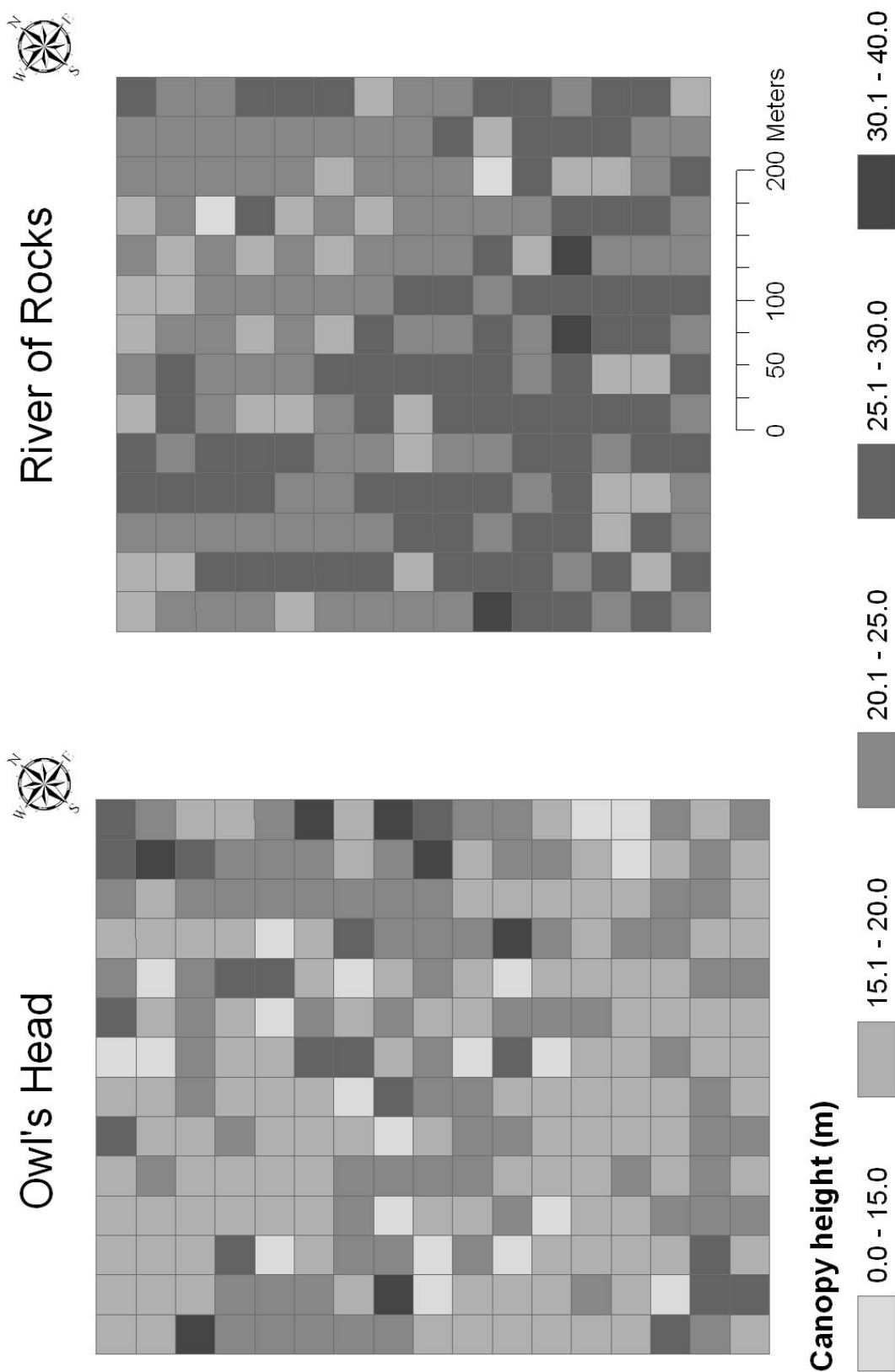
Spatial variation of green cover (total vegetative ground cover) at Owl's Head and River of Rocks study sites.

Spatial variation of litter depth at Owl's Head and River of Rocks study sites.

Owl's Head

River of Rocks

0   50   100   200 Meters

Rock cover (%)

0 - 10   11 - 23   24 - 36   37 - 49   50 - 88

Spatial variation of litter depth at Owl's Head and River of Rocks study sites.

River of Rocks

Owl's Head

Litter depth (mm)

0.0 - 20.0   20.1 - 30.0   30.1 - 40.0   40.1 - 50.0   50.1 - 81.0
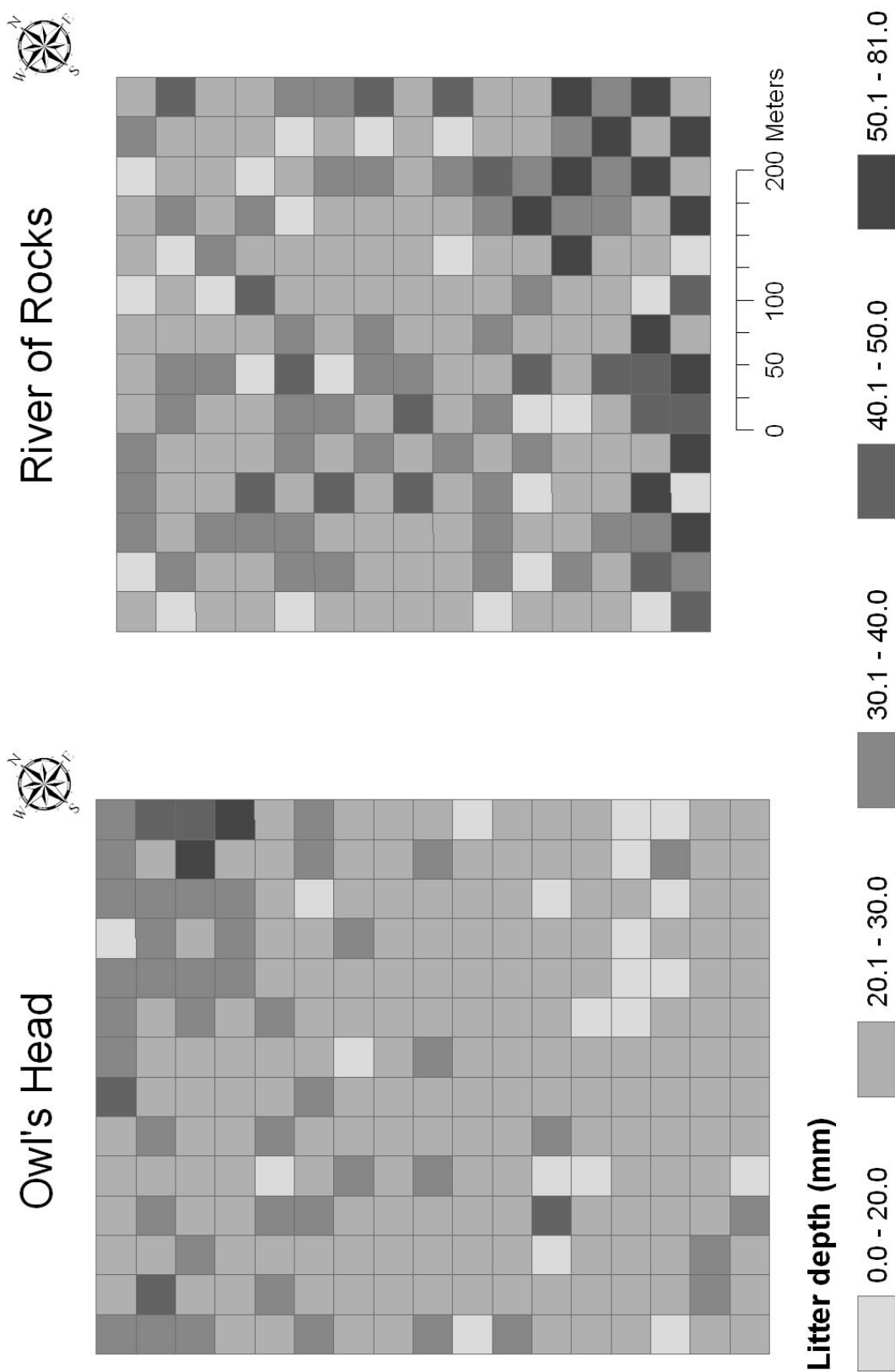
Spatial variation of small (<23 cm DBH) tree density at Owl's Head and River of Rocks study sites.

River of Rocks

Owl's Head

Small tree density (trunks per 100 sq. m)

0.0 - 5.0 5.1 - 10.0 10.1 - 15.0 15.1 - 20.0 20.1 - 37.0
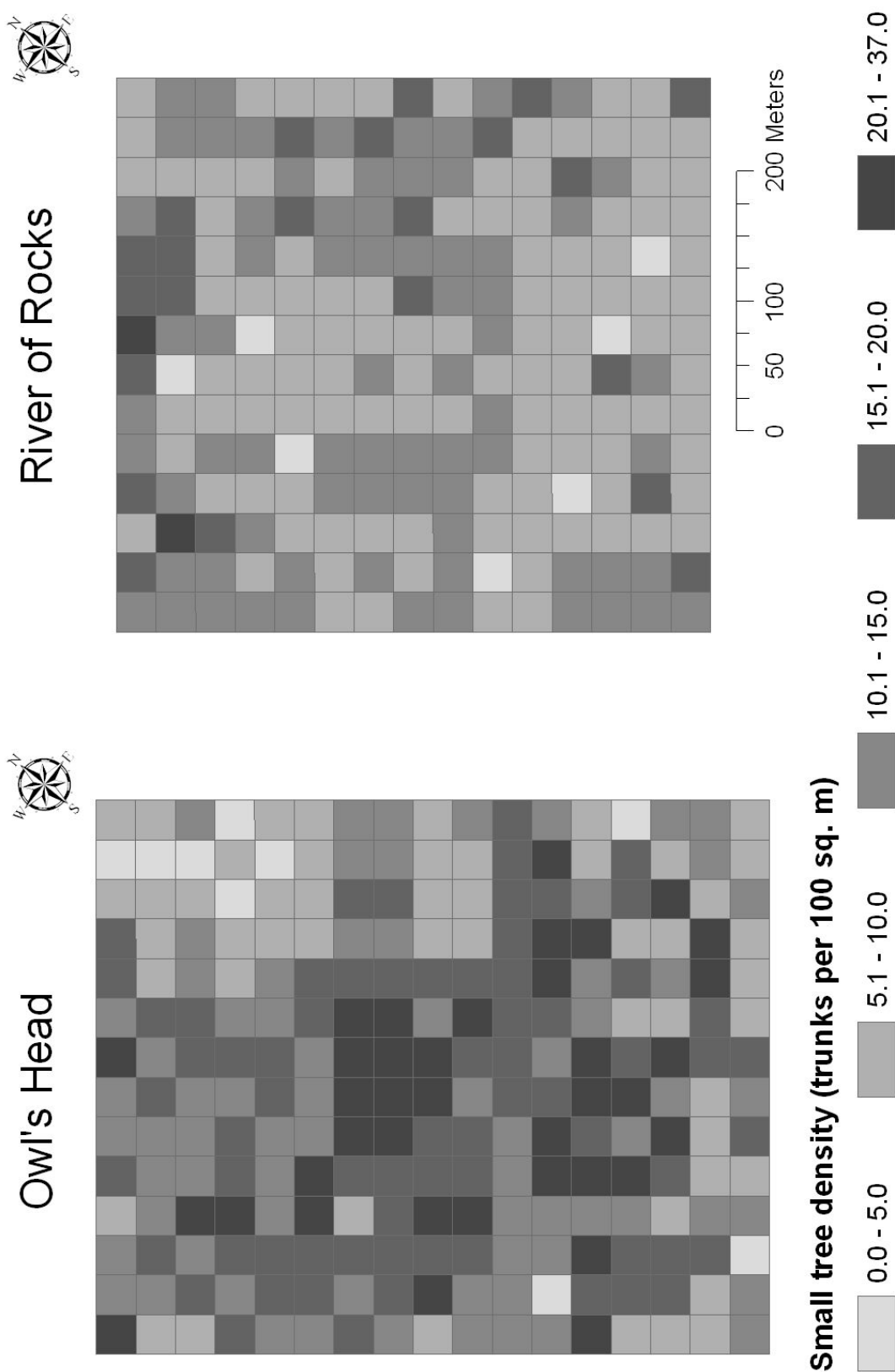
Spatial variation of large (> 23 cm DBH) tree density at Owl's Head and River of Rocks study sites.

River of Rocks

0   50   100   200 Meters

Owl's Head

Large tree density (trunks per 100 sq. m)

0.0 - 1.0   1.1 - 2.0   2.1 - 3.0   3.1 - 4.0   4.1 - 6.0
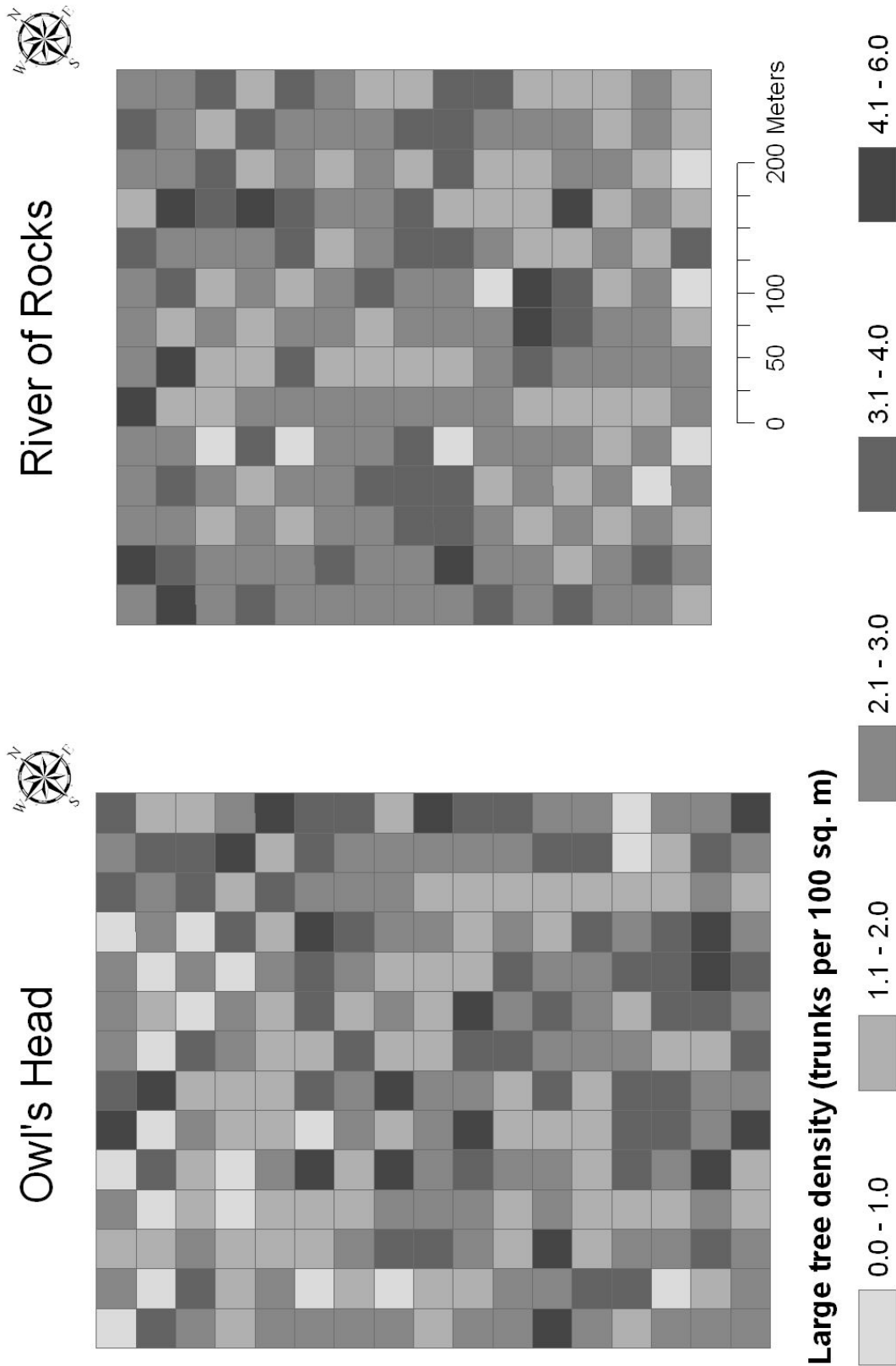
Spatial variation of snag density at Owl's Head and River of Rocks study sites.

Owl's Head

River of Rocks

Snag density (trunks per 100 sq. m)

0.0 - 1.0   1.1 - 2.0   2.1 - 3.0   3.1 - 4.0   4.1 - 6.5

0   50   100   200 Meters
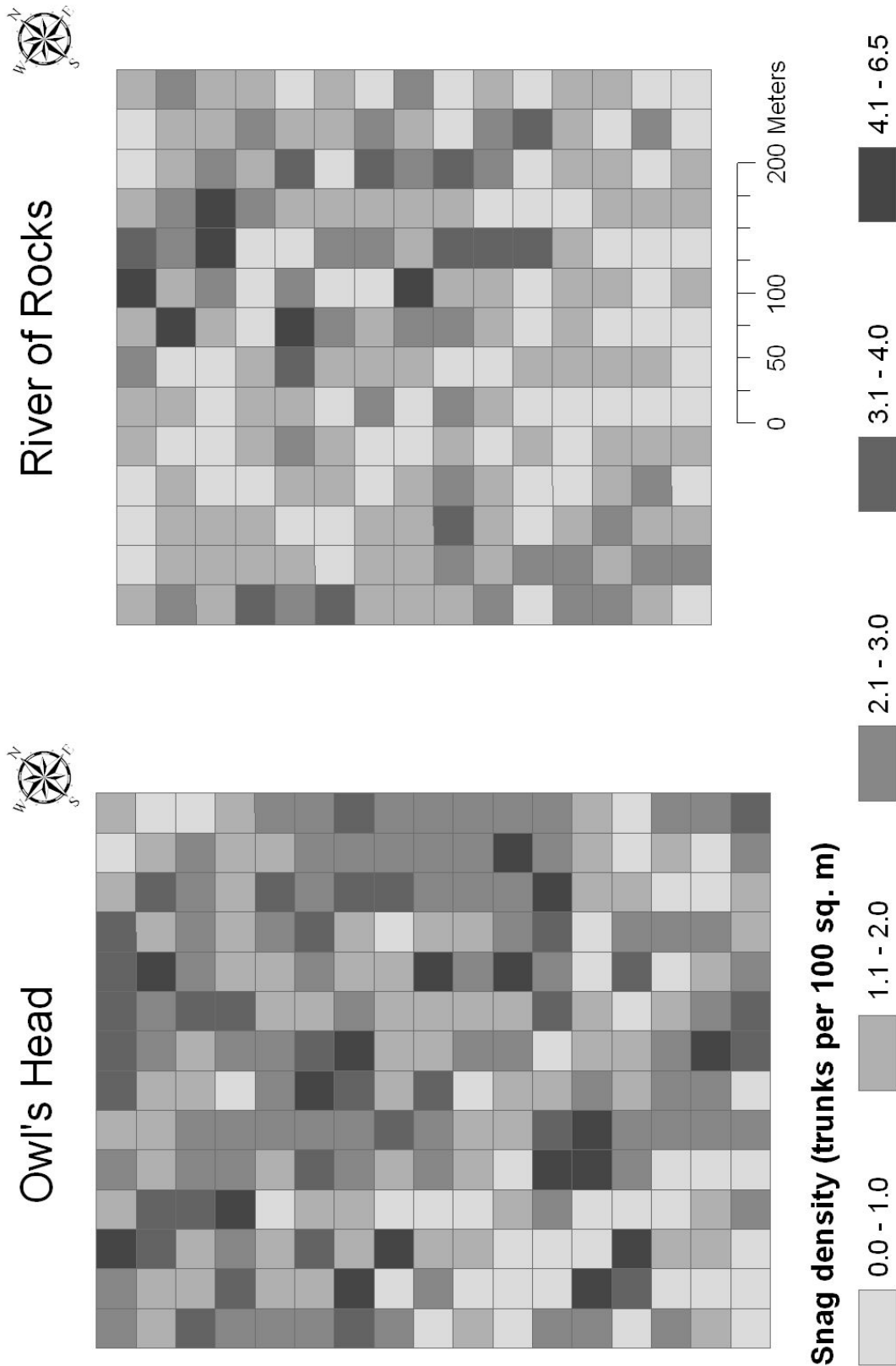
Spatial variation of shrub density at Owl's Head and River of Rocks study sites.

Shrub density (stems per 10 sq. m)

0.0 - 5.0   5.1 - 10.0   10.1 - 20.0   20.1 - 30.0   30.1 - 85.2
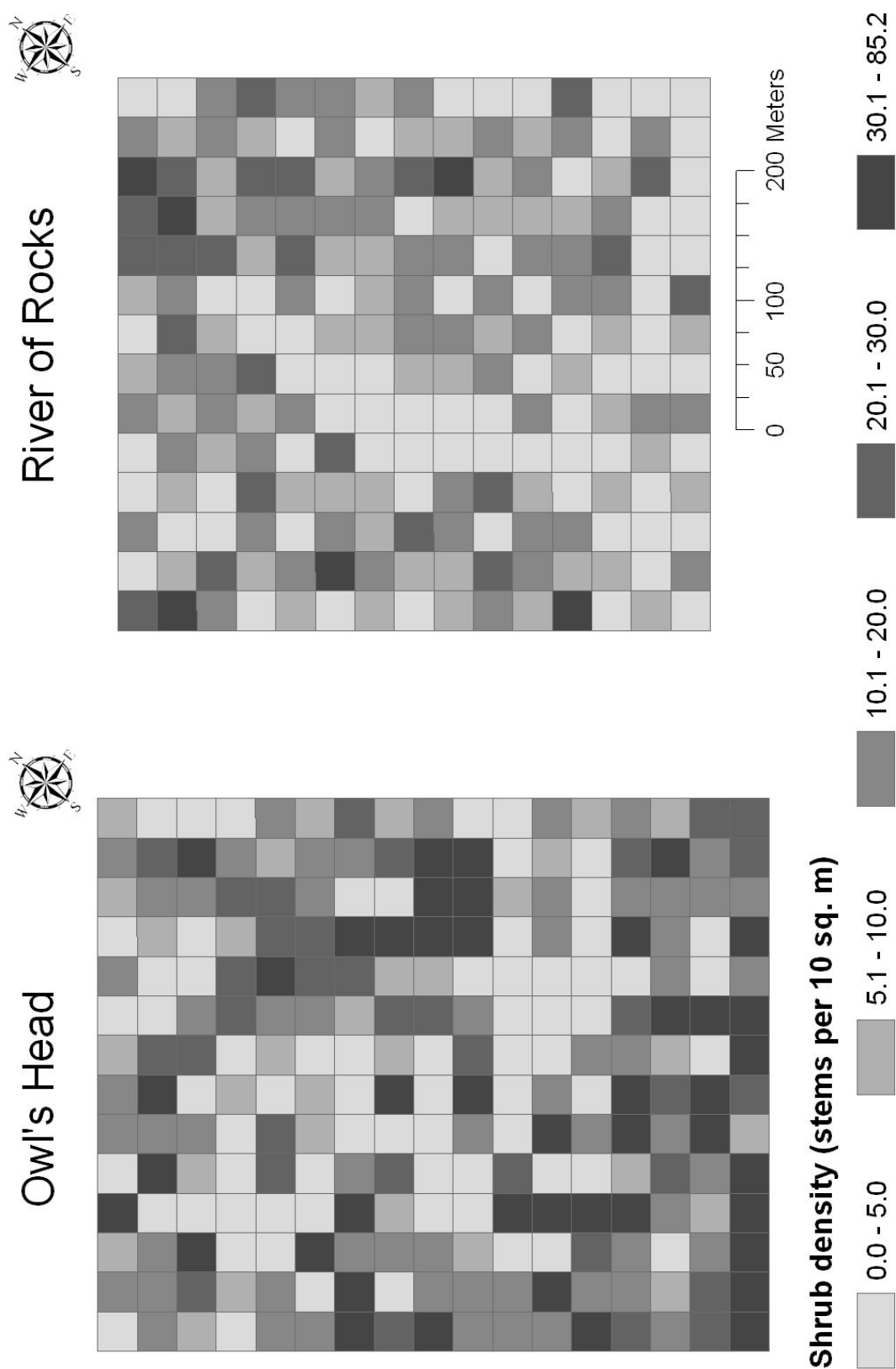
Spatial variation of slope at Owl's Head and River of Rocks study sites.

River of Rocks

Owl's Head

Slope (degrees)

| 0.0 - 3.0 | 3.1 - 6.0 | 6.1 - 9.0 | 9.1 - 12.0 | 12.1 - 15.0 |

65
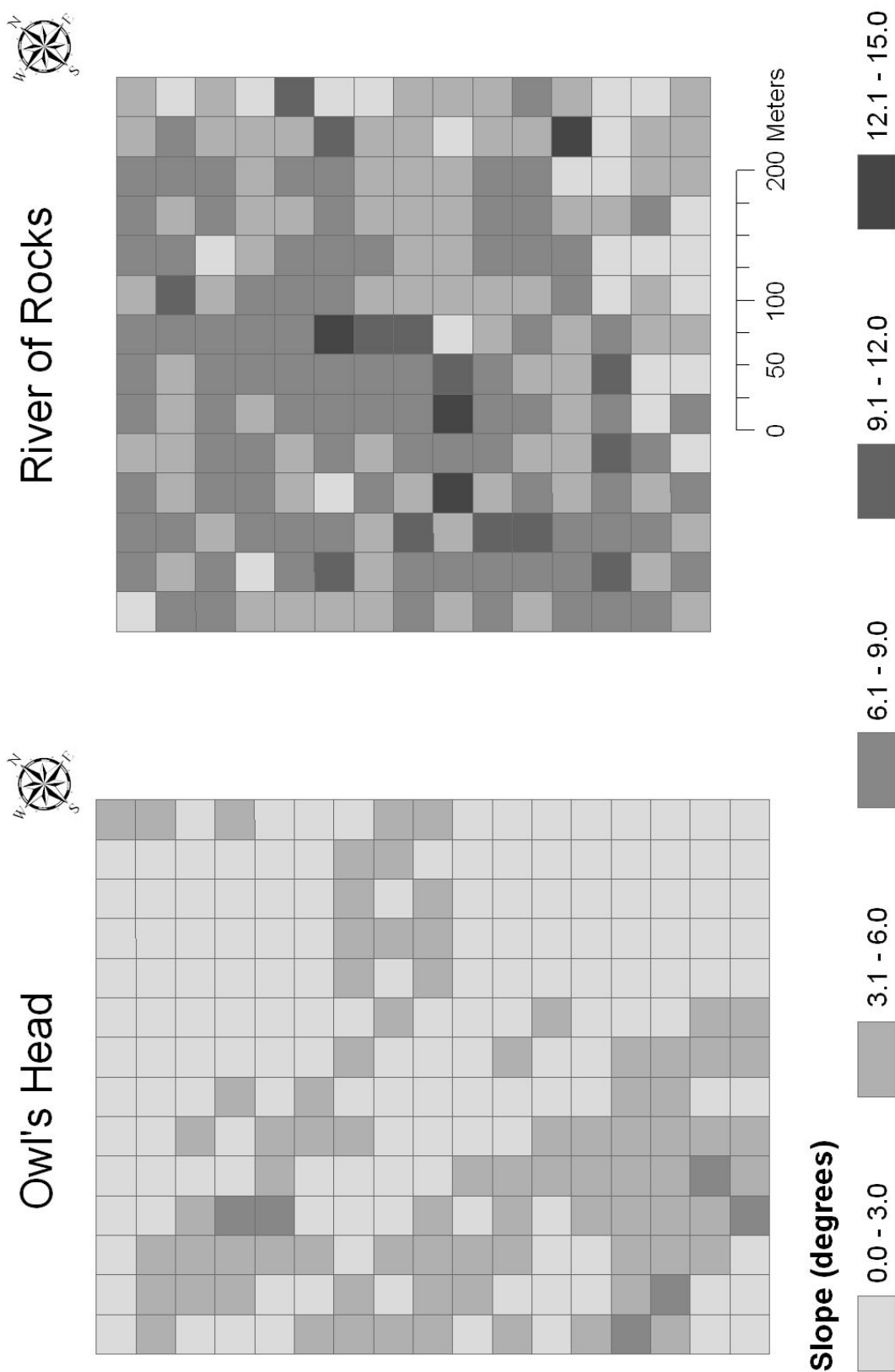
APPENDIX B

Bird Histories and Territory Maps

Reproductive success and territory data of Ovenbirds on Owl's Head study site, 1998-2009.

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
BSWW	1998	Y	Y			1	1998	2	4	10	OFF
BWSB	1998	Y	Y	33.9	0.265	1	1998	3	4	10	L04
BWSW	1998	Y	Y	46.2	0.139	4	1995	3	4	8	O07
BYSY	1998	Y	Y	99	0	1	1998	3	4	8	D05
RBYS	1998	N	N			6	1993	3	4	4	O01
SBWR	1998	Y	Y	43	0.131	1	1998	3	4	11	Q07
SWWB	1998	Y	N			1	1998	3	5	8	B05
SYRR	1998	Y	N			8	1991	3	4	10	F02
UNB	1998	N						3	5	4	A01
UNB	1998	U						2	3	3	P14
UNB	1998	U						2	3	6	M09
UNB	1998	N						4	5	6	K02
UNB	1998	U						2	3	5	A02
UNB	1998	N						3	4	3	A05
UNB	1998	U						2	3	3	A09
UNB	1998	U						2	3	5	E09
UNB	1998	U						2	3	5	I14
WYBS	1998	U	Y	94.9	0	1	1998	2	3	8	G08
BGGS	1999	Y	N			1	1999	2	7	10	N03
BSWW	1999	Y	Y	16.3	0.514	2	1998	3	6	9	E01
BWSB	1999	Y	N			2	1998	3	7	11	M05
BWSW	1999	Y	Y	57.9	0.318	5	1995	4	6	12	P07
BYSY	1999	Y	N			2	1998	1	6	11	H05
RWSY	1999	U	N			1	1999	2	4	9	G01
RYSY	1999	Y	Y	19.4	0.675	1	1999	3	5	8	K10
SBWR	1999	Y	N			2	1998	3	4	8	Q09
SGGW	1999	Y	Y	16.3	0.537	1	1999	3	8	10	A13
SRWG	1999	Y	N			2	1999	4	9	17	D03

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
SWYY	1999	Y	Y	138.3	0	1	1999	2	5	10	I13
UNB	1999	Y						2	3	5	A01
UNB	1999	N						3	8	9	B07
UNB	1999	Y						3	3	8	O05
WSWG	1999	Y	N			1	1999	2	4	12	P09
WSYR	1999	Y	Y			1	1999	1	4	12	K02
WYBS	1999	Y	Y	40	0.657	2	1998	2	4	11	F11
BRGS	2000	Y	Y			1	2000	0	3	11	L13
BSWW	2000	U	N			3	1998				OFF
BWSB	2000	Y	N			3	1998	3	5	11	M06
BYSY	2000	Y	Y	47	0.356	3	1998	7	11	21	F03
GBYS	2000	Y	N			1	2000	2	4	8	O09
RYSY	2000	U	Y	41.1	0.296	2	1999	2	4	9	J10
SBRR	2000	U	Y			1	2000				OFF
SGGW	2000	Y	Y			2	1999	2	3	13	A13
SWYY	2000	Y	N			2	1999	3	7	16	D14
UNB	2000	Y						4	6	6	J14
UNB	2000	Y						4	9	6	A08
UNB	2000	N						5	7	5	D05
UNB	2000	Y						3	7	9	B02
UNB	2000	Y						3	7	14	J03
UNB	2000	Y						4	7	8	H07
UNB	2000	Y						4	7	7	O04
WSYR	2000	U	Y			2	1999				OFF
WYBS	2000	Y	Y	42.4	0.35	3	1998	4	5	10	F10
BRGS	2001	U	Y			2	2000				OFF
BRSW	2001	U	N			2	2001	2	3	8	A12
BWGS	2001	Y	N			10	1992	1	3	12	Q09
BYSY	2001	Y	Y	19.2	0.528	4	1998	4	6	14	G02
GGSB	2001	Y	Y	34	0.405	2	2001	4	10	21	J05

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
GRSW	2001	Y	N			1	2001	7	14	17	O09
GWSY	2001	Y	Y	11.8	0.45	1	2001	3	3	8	A03
RBSG	2001	Y	Y	23.9	0.626	1	2001	5	12	10	E05
RWSG	2001	Y	N			1	2001	2	8	15	O04
RYSY	2001	Y	Y	33.1	0.298	3	1999	5	10	14	I10
SBRR	2001	N	N			2	2001	5	12	9	B07
SBYR	2001	U	N			10	1992	1	3	10	D08
SRBY	2001	Y	Y	73.3	0.157	1	2001	4	9	9	K14
SWWR	2001	U	Y	19.4	0.787	1	2001	1	5	16	P14
UNB	2001	N					2001	3	11	10	B02
UNB	2001	N						4	9	5	J02
WGBS	2001	N	Y	15.8	0.517	1	2001	5	10	12	F09
WSYR	2001	Y	N			3	1999				OFF
WYBS	2001	Y	Y	40.5	0.632	4	1998	7	8	10	F11
YBSW	2001	Y	Y	92.5	0	1	2001	2	3	11	A07
BRGS	2002	U	Y			3	2000				OFF
BSPR	2002	U	Y	19	0.377	1	2002	1	5	12	Q09
BWOS	2002	U	Y	12.7	0.584	2	2002	1	4	9	C08
BYSY	2002	N	N			5	1998	4	9	13	G02
GGSB	2002	N	Y	24.4	0.544	3	2001	5	7	13	I06
GRSO	2002	Y	Y	33.9	0.444	1	2002	4	5	13	A05
GWSY	2002	Y	Y	9.7	0.56	2	2001	5	9	12	A02
OPSR	2002	Y	Y	114	0	1	2002	4	10	10	N11
ORYS	2002	Y	Y	18.4	0.653	1	2002	4	12	10	I09
PBSO	2002	U	Y	28.7	0.197	1	2002	2	6	4	M02
PRWS	2002	Y	Y	44.6	0.088	1	2002	2	5	18	L09
PYPS	2002	Y	Y	14.2	0.421	1	2002	3	6	17	A01
RBSG	2002	Y	Y	33.5	0.563	2	2001	2	3	13	E06
RSOO	2002	N	Y	27.3	0.491	2	2002	7	12	17	J03
RYSY	2002	N	Y	34.8	0.425	4	1999	8	15	14	J11

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	FP[d]	Total	Locations	Territory center[e]
SBWG	2002	N	Y	32.2	0.081	1	2002	3	11	8	L06
SGGW2	2002	Y	Y	47.8	0.084	2	2002	2	7	18	O04
SPGG	2002	N	Y	49.3	0.01	1	2002	4	8	12	B13
SRBO	2002	Y	N			2	2002	5	9	9	O09
SRBY	2002	N	Y	46	0.145	2	2001	3	6	11	I13
SWWR	2002	Y	Y			2	2001	3	3	8	P14
UNB	2002	N						5	7	6	B02
UNB	2002	U						2	5	3	E01
UNB	2002	U						2	5	3	K14
WGBS	2002	Y	Y	47.9	0.124	2	2001	3	3	9	F09
WYBS	2002	U	Y	44.8	0.488	5	1998	0	3	11	E12
YBSW	2002	Y	Y	41.1	0.19	2	2001	2	3	10	A10
BRGS	2003	U	Y			4	2000	1	3	8	N14
BSPR	2003	Y	Y			2	2002	4	5	13	Q09
BWOS	2003	Y	Y	22.3	0.088	3	2002	5	9	13	C09
GGSB	2003	Y	Y	105.2	0	4	2001	8	11	12	H05
GRSO	2003	N	Y	10	0.409	2	2002	4	6	11	B06
GWSY	2003	Y	N			3	2001	5	8	8	A03
OPSR	2003	N	Y	61	0.053	2	2002	6	10	13	Q13
ORYS	2003	U	Y	28.8	0.284	2	2002	2	6	14	I09
OSRR	2003	Y	Y	28.7	0.521	1	2003	6	6	13	G02
PBSO	2003	N	Y	30.2	0.059	2	2002	3	4	9	L01
PRWS	2003	U	Y	50.5	0	2	2002	2	4	16	N08
PYPS	2003	N	Y	14.6	0.609	2	2002	3	6	8	A01
RBSG	2003	N	Y	21.5	0.14	3	2001	4	10	17	E05
RSOO	2003	Y	N			3	2002	5	7	14	J02
RWPS	2003	N	Y			1	2003	4	10	8	P08
RYSY	2003	Y	Y	56.5	0.13	5	1999	2	6	13	K10
SBWG	2003	Y	N			2	2002	5	9	10	M05
SGGW2	2003	Y	Y	42.9	0.243	3	2002	3	6	11	P05

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
SOWW	2003	Y	N			2	2003	2	7	7	C03
SPGG	2003	N	Y	56.5	0.159	2	2002	3	6	9	A12
SRBY	2003	U	Y	5	0.616	3	2001	2	5	11	I14
SWGB	2003	Y	N			2	2003	8	9	4	E01
SWWR	2003	U	Y			3	2001				OFF
WGBS	2003	Y	Y	59.6	0.04	3	2001	3	9	15	G09
WSPP	2003	U	Y	47.2	0.157	1	2003	0	7	15	K07
WYBS	2003	U	Y	10.4	0.745	6	1998	1	3	10	F11
YBSW	2003	Y	N			3	2001	1	4	9	A09
YOOS	2003	Y	Y	24.7	0.59	1	2003	4	11	14	A04
BBSP	2004	Y	N			2	2004	7	10	8	L08
BRGS	2004	U	Y			5	2000				OFF
BSPR	2004	Y	Y			3	2002				OFF
BWOS	2004	N	N			4	2002	3	7	6	C08
GGSB	2004	N	Y	32.9	0.068	5	2001	10	16	8	I02
GRSO	2004	N	Y	24.3	0.889	3	2002	4	7	8	A06
OPSR	2004	U	N			3	2002	2	5	18	Q11
ORYS	2004	N	Y	39.6	0	3	2002	3	8	15	I08
OSRR	2004	Y	Y	10.8	0.402	2	2003	6	11	11	F01
PBSO	2004	Y	Y	70.1	0	3	2002	5	12	11	M02
PRWS	2004	Y	Y	32.9	0.073	3	2002	4	6	9	O08
PYPS	2004	Y	Y	56.8	0.001	3	2002	5	10	8	A02
RBSG	2004	Y	Y	30.3	0.311	4	2001	5	13	10	E04
RWPS	2004	U	N			2	2003				OFF
RYSY	2004	Y	Y	78.9	0	6	1999	6	8	8	I11
SGGW2	2004	Y	Y	73.2	0.058	4	2002	4	9	9	P04
SPGG	2004	Y	N			3	2002	5	8	12	A10
SRBY	2004	Y	N			4	2001	4	7	9	I14
SWWR	2004	N	Y			4	2001	3	5	10	P14
WGBS	2004	Y	Y	49.7	0.166	4	2001	6	11	8	E08

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
WSPP	2004	N	N			2	2003	4	12	12	K06
WYBS	2004	N	Y	25.9	0.502	7	1998	3	7	16	F11
YOOS	2004	Y	Y	37.9	0.043	2	2003	4	10	14	A03
BRGS	2005	Y	Y			6	2000				OFF
BSPR	2005	Y	Y	20.4	0.929	4	2002	3	5	12	M14
GGSB	2005	Y	Y	35.8	0.011	6	2001	4	6	9	Q10
GRSO	2005	Y	Y	27.6	0.131	4	2002	5	7	23	I03
ORYS	2005	N	N			4	2002	8	10	11	A07
OSRR	2005	Y	Y	11.4	0.833	3	2003	4	5	10	H09
PBSO	2005	Y	Y	32.6	0.268	4	2002	7	8	11	E01
PRWS	2005	Y	N			4	2002	5	6	14	M05
PSYO	2005	N	Y	21	0.188	1	2005	3	5	13	P08
PYPS	2005	N	Y	40.2	0.189	4	2002	5	6	8	A12
RBSG	2005	Y	Y	17.4	0.703	5	2001	8	12	19	C02
RORS	2005	Y	N			1	2005	6	10	12	E05
RYSY	2005	Y	Y	24.6	0.569	7	1999	5	7	10	K11
SGGW2	2005	Y	Y	38	0.369	5	2002	7	9	23	I14
SRBR	2005	Y	Y	20.2	0.384	1	2005	11	12	18	K06
SWWR	2005	U	N			5	2001				OFF
WGBS	2005	Y	Y	72.6	0.007	5	2001	7	9	12	F06
WPSB	2005	Y	Y	41.8	0.099	1	2005	10	11	12	N11
WYBS	2005	N	Y	32.2	0.727	8	1998	4	5	14	E11
YOOS	2005	Y	Y	40	0	3	2003	7	10	10	A02
BOBS	2006	Y	Y	12.2	0.864	1	2006	2	6	11	J10
BOGS	2006	Y	Y	1.8	0.863	1	2006	3	4	9	A06
BRGS	2006	U	N			7	2000				OFF
BSPR	2006	Y	N			5	2002	6	7	9	Q11
GGSB	2006	N	N			7	2001	6	10	10	J02
GRSO	2006	N	Y	71.9	0	5	2002	6	9	12	A08
OSRR	2006	Y	Y	8.4	0.345	4	2003	12	16	15	F01

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Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
PBSO	2006	Y	Y	49.8	0.048	5	2002	7	8	11	M04
PSBW	2006	U	Y			1	2006				OFF
PSGR	2006	U	Y	113	0	1	2006	2	4	13	H06
PSOP	2006	N	N			1	2006	3	6	10	L12
PSYO	2006	Y	Y	24.6	0.917	2	2005	4	8	10	A12
PYPS	2006	Y	Y	30.9	0.653	5	2002	9	14	10	B01
RBSG	2006	Y	N			6	2001	6	12	15	E05
RYSY	2006	Y	Y	29.3	0.19	8	1999	6	10	15	H13
SBRW	2006	Y	Y	38.1	0.372	1	2006	5	8	12	C11
SGGW2	2006	Y	N			6	2002	7	12	10	O05
SRBR	2006	Y	Y	84.6	0	2	2005	4	6	12	J06
UNB	2006	U						2	3	6	P08
WGBS	2006	Y	Y	45.7	0.317	6	2001	7	12	11	G05
WORS	2006	N	N			1	2006	6	7	15	N05
WPSB	2006	Y	Y	47.3	0.169	2	2005	5	9	9	O09
WSOO	2006	Y	N			1	2006	3	7	12	M07
WWPS	2006	Y	N			1	2006	8	13	15	B08
WYBS	2006	N	Y	22.6	0.669	9	1998	3	7	16	F11
YGSO	2006	Y	N			1	2006	4	11	10	F08
YOOS	2006	Y	Y	35.1	0.257	4	2003	5	9	9	A03
YRPS	2006	U	Y			1	2006	2	3	9	P01
YYSP	2006	N	Y	26.2	0.272	1	2006	3	6	13	P13
BOBS	2007	Y	Y	37.7	0.439	2	2006	7	9	14	J10
BOGS	2007	Y	N			2	2006	7	9	11	A06
GRSO	2007	Y	Y	16.9	0.797	6	2002	11	14	18	C07
OSRR	2007	Y	Y	28.7	0.13	5	2003	3	5	8	F01
PBSO	2007	Y	N			6	2002	4	10	18	L02
PSBW	2007	U	Y			2	2006				OFF
PSGR	2007	Y	Y	12.3	0.567	2	2006	4	9	11	G03
PSYO	2007	Y	Y	7.3	0.773	3	2005	9	11	16	A12

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
PWSY	2007	Y	Y	11.7	0.742	1	2007	7	10	25	I03
PYPS	2007	N	Y	41.3	0.153	6	2002	6	11	18	B02
RRSP	2007	Y	Y	8	0.384	1	2007	12	14	21	F09
RSRO	2007	N	Y	45.6	0.691	1	2007	3	6	12	P04
RYPS	2007	Y	Y	18.1	0.507	1	2007	6	8	8	Q08
RYSY	2007	U	N			9	1999	0	5	10	I14
SBRW	2007	N	Y	18	0.4	2	2006	6	9	17	C10
SGYY	2007	N	Y	25	0.963	1	2008	14	16	9	D02
SRBR	2007	N	Y	21	0.648	3	2005	3	4	17	M05
UNB	2007	U						2	4	12	C13
WGBS	2007	Y	Y	35.7	0.284	7	2001	13	17	13	F06
WPSB	2007	Y	Y	29.2	0.747	3	2005	3	7	13	O08
WYBS	2007	Y	Y	47.3	0.037	10	1998	4	5	16	F11
YOOS	2007	Y	N			5	2003	9	15	15	A02
YRPS	2007	U	N			2	2006				OFF
YYSP	2007	Y	Y	36.9	0.198	2	2006	4	5	14	Q12
YYSW	2007	N	Y	35.5	0.843	1	2007	6	8	14	I07
BOBS	2008	Y	Y	19.7	0.301	3	2006	5	8	18	J12
GRSO	2008	Y	Y	10.6	0.803	7	2002	9	18	35	B07
OSRR	2008	Y	Y			6	2003	4	7	9	E01
PSBW	2008	Y	Y			3	2006				OFF
PSGR	2008	U	Y	32.3	0.077	3	2006	2	4	19	A01
PSYO	2008	U	Y	13.6	0.821	4	2005	1	5	14	G02
PWSY	2008	Y	Y	12.7	0.678	2	2007	9	13	25	A12
PYPS	2008	Y	Y	30	0.438	7	2002	5	10	21	J03
RRSP	2008	Y	Y	29.9	1	2	2007	5	10	16	F10
RSRO	2008	Y	Y	19.1	0.575	2	2007	9	16	44	O03
RYPS	2008	N	Y	21.2	0.088	2	2007	7	10	10	Q07
SBRW	2008	Y	Y	144.2	0	3	2006	5	7	13	B11
SGYY	2008	N	Y	11.8	0.219	2	2008	9	19	29	D03

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Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
SRBR	2008	Y	Y	28.8	0.475	4	2005	5	11	18	M05
SYOY	2008	U	Y	154.4	0	1	2008	0	5	9	D08
WGBS	2008	Y	Y	26.9	0.602	8	2001	6	12	22	F05
WPSB	2008	Y	Y	20.5	0.971	4	2005	8	13	23	O09
WYBS	2008	Y	N			11	1998	5	6	11	G12
YYSP	2008	N	N			3	2006	5	6	13	P12
YYSW	2008	N	N			2	2007	8	18	20	J08
BOBS	2009	Y				4	2006	4	12	18	K11
GRSO	2009	Y				8	2002	10	16	34	B07
OSRR	2009	U				7	2003				OFF
PSBW	2009	Y				4	2006				OFF
PSGR	2009	Y				4	2006	8	12	11	A01
PSYO	2009	N				5	2005	10	16	21	G02
PWSY	2009	Y				3	2007	9	19	25	A12
PYPS	2009	Y				8	2002	9	19	25	J03
RRSP	2009	Y				3	2007	8	12	26	B02
RSRO	2009	Y				3	2007	8	14	16	F10
RYPS	2009	Y				3	2007				OFF
SBRW	2009	N				4	2006	8	12	24	O04
SGYY	2009	Y				3	2008	5	13	14	Q07
SRBR	2009	Y				5	2005	3	10	18	F14
SRYW	2009	Y				1	2009	7	13	14	D03
SYOY	2009	Y				2	2008	5	11	20	M04
UNB	2009	Y						3	6	9	P13
UNB	2009	Y						8	12	13	I08
UNB	2009	Y						9	11	22	Q01
UNB	2009	N						7	12	11	I13
WGBS	2009	Y				9	2001	8	15	14	E12
WPSB	2009	N				5	2005	10	20	34	A05

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Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
BGWS	1998	U	N			1	1998	2	4	8	C14
GRSR	1998	U	Y	209.6	0	1	1998	1	3	8	B08
GSGG	1998	Y	Y	98.2	0	1	1998	1	3	8	L01
RBSW	1998	U	Y			1	1998	2	3	8	O05
RRBS	1998	Y	N			1	1998	1	3	10	N10
SRRB	1998	U	Y	29	0.367	1	1998	2	4	16	L14
SRRR	1998	Y	Y			1	1998				OFF
SWBR	1998	Y	Y			1	1998				OFF
UNB	1998	Y						3	4	5	I06
UNB	1998	U						2	4	11	G03
UNB	1998	U						2	4	5	D03
UNB	1998	N						4	5	22	G13
BYWS	1999	U	N			2	1999	2	3	8	G06
GRSR	1999	Y	Y	133.5	0	2	1998	2	4	12	F03
GSBR	1999	U	Y			1	1999	1	3	9	C06
GSGG	1999	Y	Y	74.4	0.011	2	1998	2	4	10	O03
RBSW	1999	Y	N			2	1998				OFF
RSYR	1999	U	N			2	1999	2	3	10	K04
SGYR	1999	Y	Y			1	1999				OFF
SRRB	1999	N	N			2	1998	3	5	9	L13
SRRR	1999	Y	N			2	1998	5	7	8	L01
SWBR	1999	Y	N			2	1998	3	4	8	B02
UNB	1999	U						1	3	8	I12
WSWB	1999	U	Y			2	1999				OFF
BGYS	2000	Y	Y	69.5	0.11	1	2000	2	4	13	O04
GRSR	2000	Y	Y	66.5	0.261	3	1998	4	6	14	B03
GSBR	2000	U	N			2	1999				OFF
GSGG	2000	Y	Y	19.8	0.277	3	1998	4	6	15	L02

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Total	Locations	Territory center[e]
SGBY	2000	N	Y	55.5	0.029	1	2000	3	5	10	K05
SGYR	2000	Y	Y	60.1	0.229	2	1999	6	7	22	F04
UNB	2000	N						4	5	4	N12
UNB	2000	Y						6	9	16	C13
UNB	2000	Y						6	9	15	F11
WSWB	2000	Y	N			3	1999	1	3	12	M06
BGYS	2001	U	N			2	2000	2	3	8	O01
GBSG	2001	N	N			1	2001	4	7	8	C13
GRSR	2001	Y	Y	7.2	0.156	4	1998	4	9	9	C05
GSGG	2001	Y	Y	20.9	0.448	4	1998	5	10	10	M02
RBGS	2001	Y	Y	55.1	0.417	1	2001	1	3	18	M13
RSWG	2001	N	Y	87.1	0	1	2001	4	8	13	N09
SGBY	2001	Y	Y	84.2	0	2	2000	6	10	10	M04
SGYR	2001	Y	Y	23.4	0.294	3	1999	1	5	15	H04
SWGG	2001	Y	Y	42.5	0.385	1	2001	5	11	15	J13
SYRW	2001	U	N			1	2001	2	6	12	K08
WBSB	2001	Y	N			1	2001	5	9	10	O05
WBSW	2001	Y	Y	86.9	0	1	2001	6	10	21	G12
YRSW	2001	Y	N			1	2001	4	6	10	O14
BBSO	2002	Y	N			1	2002	5	13	15	H05
GRSR	2002	Y	Y	48.6	0.372	5	1998	5	9	11	C05
GSGG	2002	Y	Y	15.3	0.876	5	1998	5	9	16	M03
GSYY	2002	Y	Y	71.4	0	2	2002	2	7	9	O14
GWBS	2002	N	Y	124.7	0	1	2002	4	10	13	L04
RBGS	2002	Y	Y	9.1	0.511	2	2001	8	12	18	K14
RSWG	2002	N	N			2	2001	3	8	15	O11
SBOO	2002	Y	N			1	2002	5	10	12	N09
SGBY	2002	Y	Y	29.5	0.503	3	2000	7	12	15	O03
SGYR	2002	Y	Y	40.5	0.393	4	1999	6	13	18	I03
SOOO	2002	Y	Y	41.4	0.233	1	2002	6	13	25	O05

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Total	Locations	Territory center[e]
SPPB	2002	N	N			1	2002	6	11	12	B12
SWGG	2002	Y	Y	22.4	0.312	2	2001	7	12	30	H13
UNB	2002	Y						4	7	7	D11
WBSW	2002	N	Y	27.6	0.726	2	2001	3	7	15	E14
GRSR	2003	Y	Y	16.9	0.513	6	1998	4	7	12	B04
GSGG	2003	Y	Y	51.3	0.148	6	1998	5	8	21	M03
GSYY	2003	N	Y	15.6	0.167	3	2002	4	6	8	L14
GWBS	2003	Y	N			2	2002	4	6	8	I07
OGSY	2003	N	N			1	2003	3	6	8	D10
ORPS	2003	N	Y	19.1	0.743	2	2003	5	7	10	O14
PPRS	2003	Y	Y	3.3	0.209	2	2003	4	7	14	O10
RBGS	2003	Y	Y	19.8	0.413	3	2001	4	5	10	K13
SGBY	2003	N	Y	26.3	0.146	4	2000	3	6	15	O04
SGYR	2003	Y	Y	14.4	0.824	5	1999	3	5	9	H04
SOOO	2003	Y	Y	6.5	0.631	2	2002	2	5	15	N06
SWGG	2003	Y	Y	38.9	0.56	3	2001	2	5	12	H12
WBSW	2003	U	N			3	2001	0	3	12	D13
GRSR	2004	Y	N			7	1998	4	6	17	B04
GSGG	2004	Y	N			7	1998	4	8	25	K03
GSYY	2004	Y	N			4	2002	3	7	10	M14
ORPS	2004	Y	Y	16.3	0.498	3	2003	4	9	11	O13
PPRS	2004	Y	Y	111.2	0	3	2003	5	9	11	O10
RBGS	2004	Y	N			4	2001	2	9	12	L13
SGBY	2004	Y	N			5	2000	4	5	11	O05
SGYR	2004	N	N			6	1999	5	8	18	H04
SOOO	2004	Y	Y	41.1	0.158	3	2002	2	6	10	N06
SRPP	2004	Y	Y	46.9	0.087	2	2004	3	6	11	E05
SWGG	2004	Y	Y	61.1	0.489	4	2001	7	13	24	G12
BYSP	2005	Y	N			2	2005	1	4	11	E02
ORPS	2005	Y	N			4	2003	9	11	10	O13

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
PGSB	2005	Y	N			1	2005	7	9	10	M08
PPRS	2005	N	N			4	2003	3	4	14	L11
PSPW	2005	Y	N			1	2005	9	10	14	O09
RROS	2005	Y	Y	248.5	0	1	2005	7	10	16	C14
SOOO	2005	N	N			4	2002	15	21	34	M05
SRPP	2005	Y	Y	15.6	0.316	3	2004	5	9	16	G05
SWGG	2005	Y	N			5	2001	7	11	21	I12
SYOW	2005	Y	Y			2	2005	7	9	15	H06
UNB	2005	N						6	6	8	D10
WPYS	2005	U	Y	60.8	0.226	1	2005	2	5	8	M01
WYSG	2005	Y	N			1	2005	5	8	14	J03
YSGR	2005	Y	N			1	2005	4	5	8	B03
BOSR	2006	U	N			1	2006	2	5	8	B03
BPBS	2006	Y	Y	40.3	0.209	1	2006	7	12	11	N09
GOSY	2006	Y	N			1	2006	5	7	8	O06
OSYO	2006	Y	Y	32.2	0.432	1	2006	5	9	8	D01
POSW	2006	N	Y	105	0	1	2006	5	7	15	N06
RROS	2006	Y	Y	34.2	0.361	2	2005	10	16	16	K13
RSBP	2006	Y	Y	106.7	0	1	2006	9	14	14	G02
SRPP	2006	Y	N			4	2004	9	15	9	G05
SYOW	2006	U	Y			3	2005			13	OFF
WGSG	2006	Y	Y	73	0.527	1	2006	9	14	13	J03
WPYS	2006	N	N			2	2005	8	13	19	N03
WSWP	2006	Y	Y	64.1	0.355	1	2006	8	12	10	E14
WWSY	2006	Y	Y	65.1	0	1	2007	6	10	3	I12
BPBS	2007	U	N			2	2006	0	3	20	O09
OSYO	2007	Y	Y	26.2	0.682	2	2006	5	11	27	E02
POSW	2007	U	N			2	2006	1	5	9	N03
RROS	2007	Y	Y	26.5	0.687	3	2005	5	12	18	L14
RSBP	2007	N	Y	69	0	2	2006	5	10	27	G06

79

Band combination[a]	Year	Success[b]	Return[c]	Shift distance (m)	Territory overlap (prop.)	Age (yrs)	Band year	Observations FP[d]	Observations Total	Locations	Territory center[e]
SYOW	2007	U	N			4	2005	0	3	14	O13
WGSG	2007	U	Y	31.3	0.502	2	2006	1	5	15	L05
WSWP	2007	Y	Y	21.5	0.818	2	2006	4	8	13	C14
WWSY	2007	Y	Y	90.6	0.23	2	2007	3	8	21	G13
YSYG	2007	U	N			2	2007	1	4	8	O05
OSYO	2008	N	Y	64.4	0.279	3	2006	7	9	19	F02
OWSB	2008	N	N			1	2008	5	12	24	M08
RROS	2008	N	Y	23.2	0.434	4	2005	7	10	26	L14
RSBP	2008	U	N			3	2006	0	3	6	G04
SOGG	2008	Y	N			1	2008	2	5	8	B07
UNB	2008	U						0	3	8	H01
WGSG	2008	N	N			3	2006	3	6	26	K04
WSWP	2008	Y	N			3	2006	4	11	22	C14
WWSY	2008	Y	N			3	2007	3	6	25	F11
YBOS	2008	Y	N			1	2008	3	4	10	B04
OSYO	2009	Y				4	2006	9	15	26	F04
RROS	2009	Y				5	2005	11	18	21	M14
SPBB	2009	U				1	2009	2	8	9	I02
UNB	2009	Y						10	17	30	N05
UNB	2009	Y						8	15	16	O11
UNB	2009	N						9	14	7	I06
UNB	2009	N						9	12	22	B04
UNB	2009	Y						16	26	36	D12
UNB	2009	N						6	8	8	L01
YPSW	2009	U				1	2009	1	7	6	C05

aLetters correspond to band colors (B = blue, G = green, O = orange, P = purple, R = red, S = silver aluminum U.S. Fish and Wildlife

Service band, W = white, Y = yellow). Bands were read in the following order: top left, bottom left, top right, bottom right.

Unbanded birds were indicated by "UNB."

bY = Yes (successful), N = No (unsuccessful), U = Unknown

cY = Yes (returned), N = No (failed to return)

dNumber of observations during the fledgling period, mid-June to mid-July.

eGrid point closest to the territory center. OFF indicates territory was completely outside of the study site.
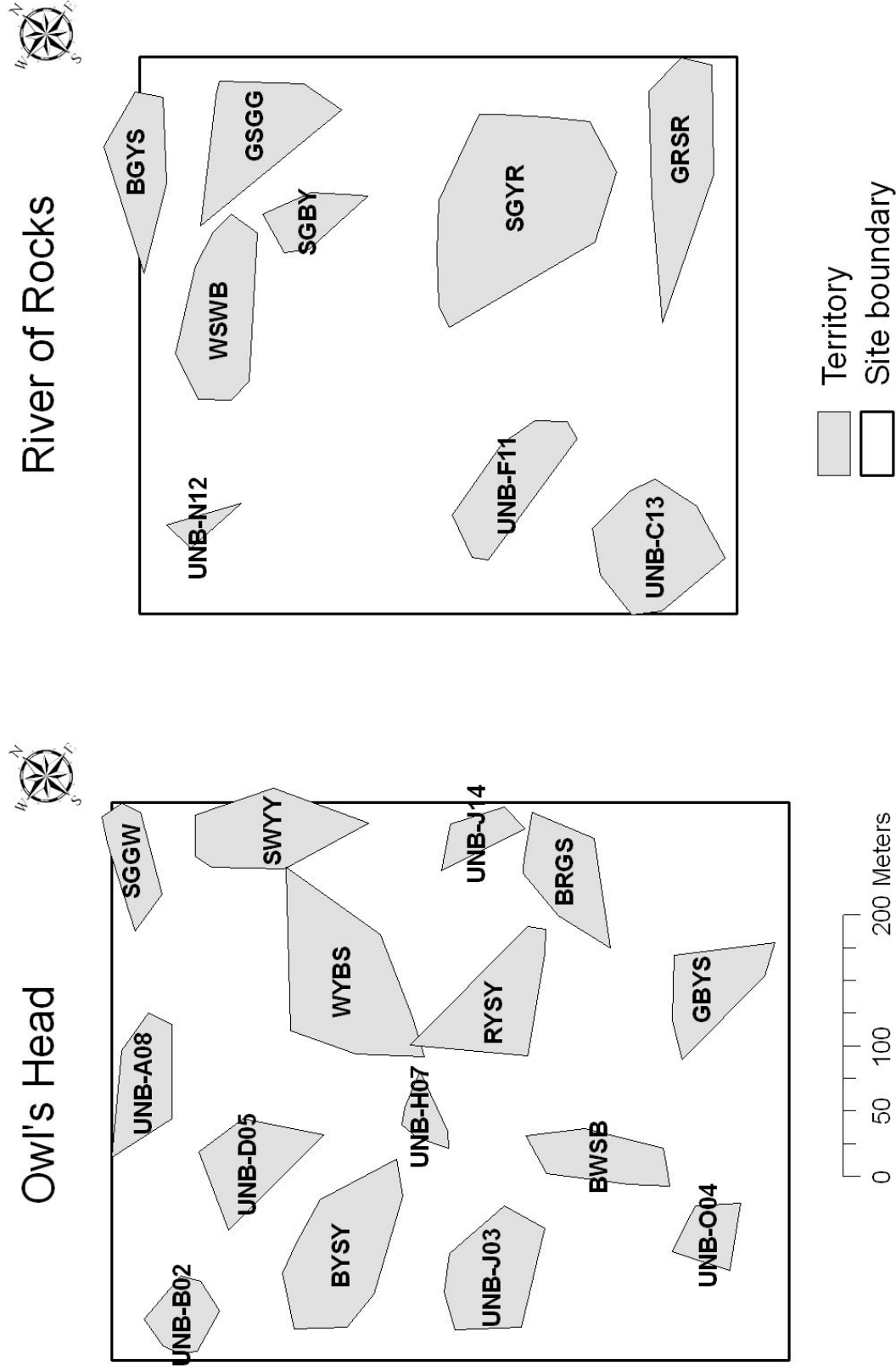
Territories defended by birds at Owl's Head and River of Rocks sites during the 1998 season. Bird names correspond to color band combination (B = blue, G = green, O = orange, P = purple, R = red, S = silver aluminum U.S. Fish and Wildlife Service band, W = white, Y = yellow). Unbanded birds are indicated by "UNB" and identified by location based on the nearest grid point.
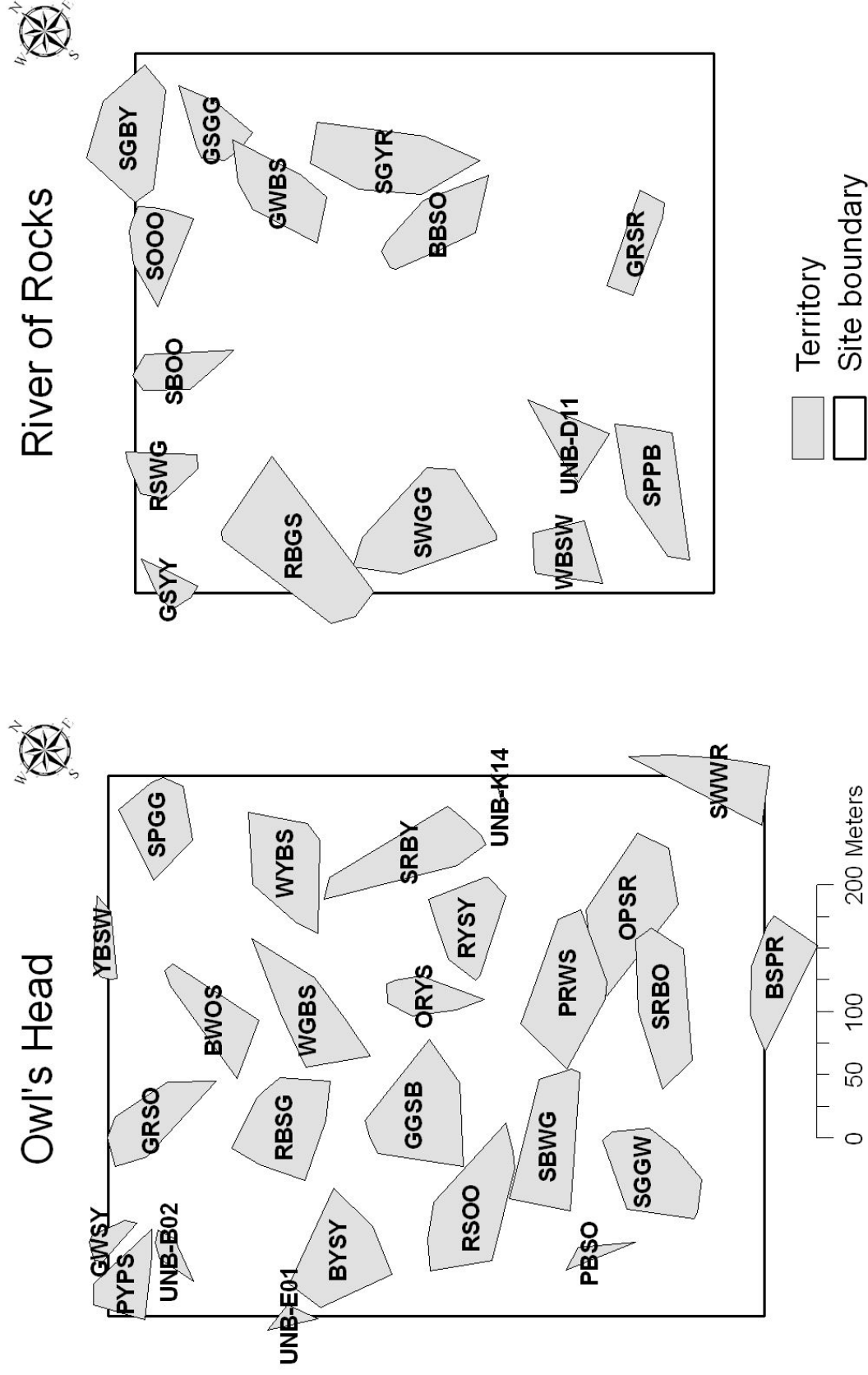
River of Rocks

Owl's Head

Territory

Site boundary

0   50   100   200 Meters
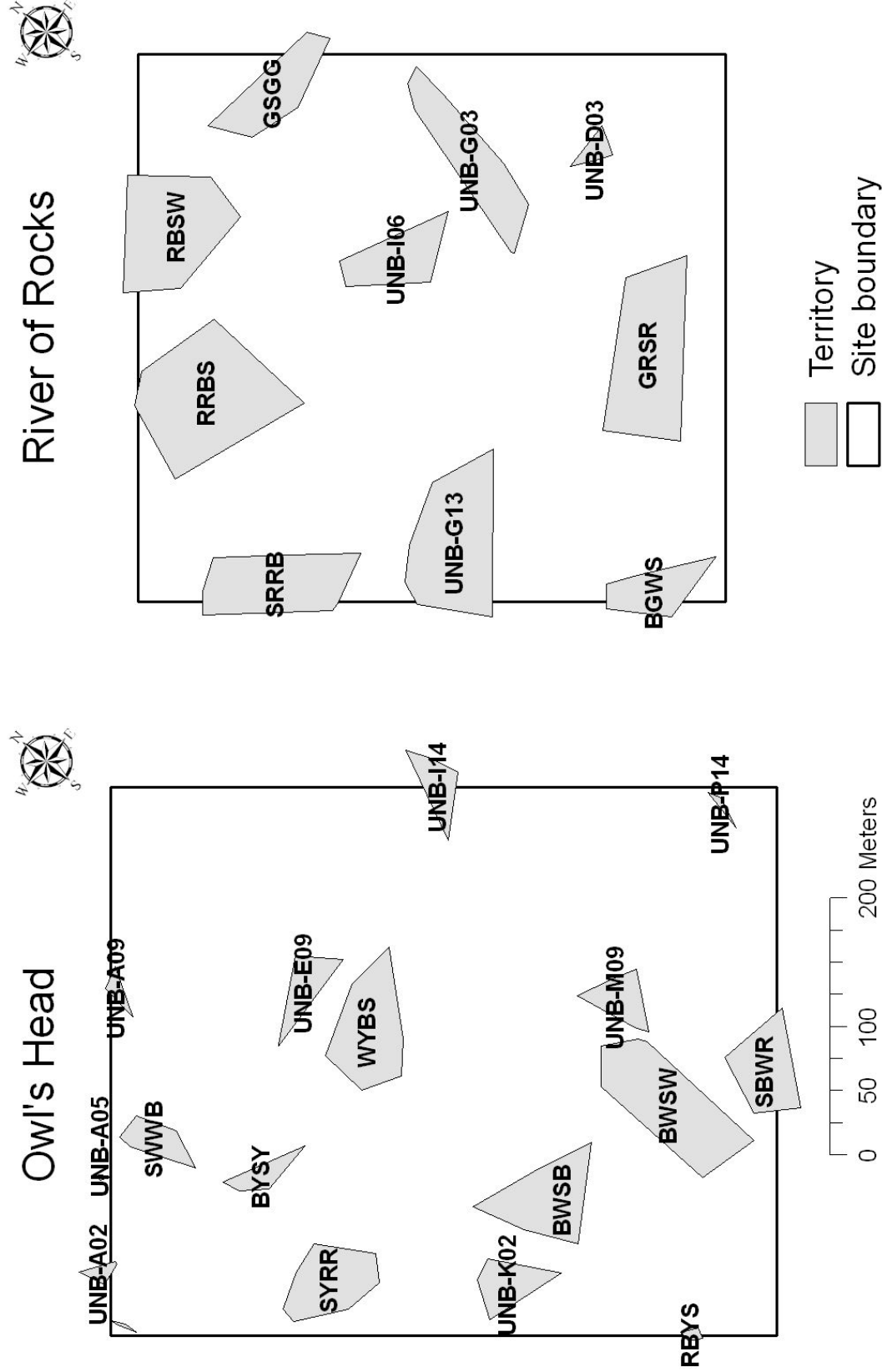
Territories defended by birds at Owl's Head and River of Rocks sites during the 1999 season.

Owl's Head

River of Rocks

Territory
Site boundary

200 Meters

0   50   100
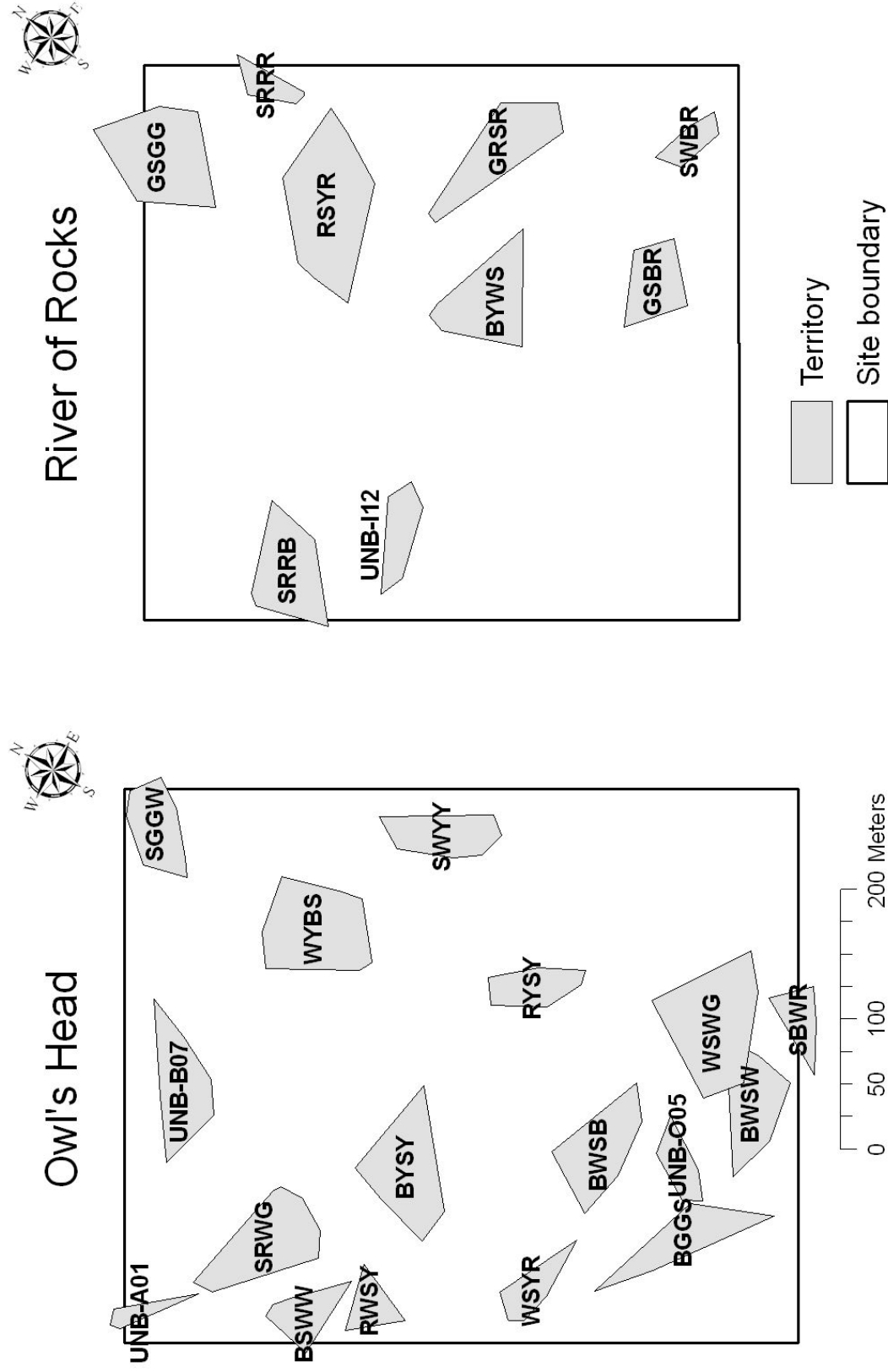
Territories defended by birds at Owl's Head and River of Rocks sites during the 2000 season.

River of Rocks

BGYS

GSGG

SGBY

WSWB

UNB-N12

SGYR

GRSR

UNB-F11

UNB-C13

Territory

Site boundary

Owl's Head

SGGW

SWYY

UNB-J14

BRGS

WYBS

RYSY

GBYS

UNB-A08

UNB-D05

UNB-H07

BWSB

UNB-B02

BYSY

UNB-J03

UNB-O04

0   50   100   200 Meters

Territories defended by birds at Owl's Head and River of Rocks sites during the 2001 season.

Owl's Head

GWSY
PYPS
UNB-B02
UNB-E01
BYSY
GRSO
RBSG
BWOS
WGBS
GGSB
RSOO
SBWG
SGGW
PBSO
SPGG
WYBS
SRBY
UNB-K14
ORYS
RYSY
PRWS
OPSR
SRBO
BSPR
SWWR
YBSW

0   50   100   200 Meters

River of Rocks

GSYY
RSWG
SBOO
SOOO
SGBY
GSGG
GWBS
SGYR
BBSO
GRSR
RBGS
SWGG
WBSW   UNB-D11
SPPB

Territory
Site boundary

85

Territories defended by birds at Owl's Head and River of Rocks sites during the 2002 season.

Owl's Head

River of Rocks

Territory
Site boundary

86
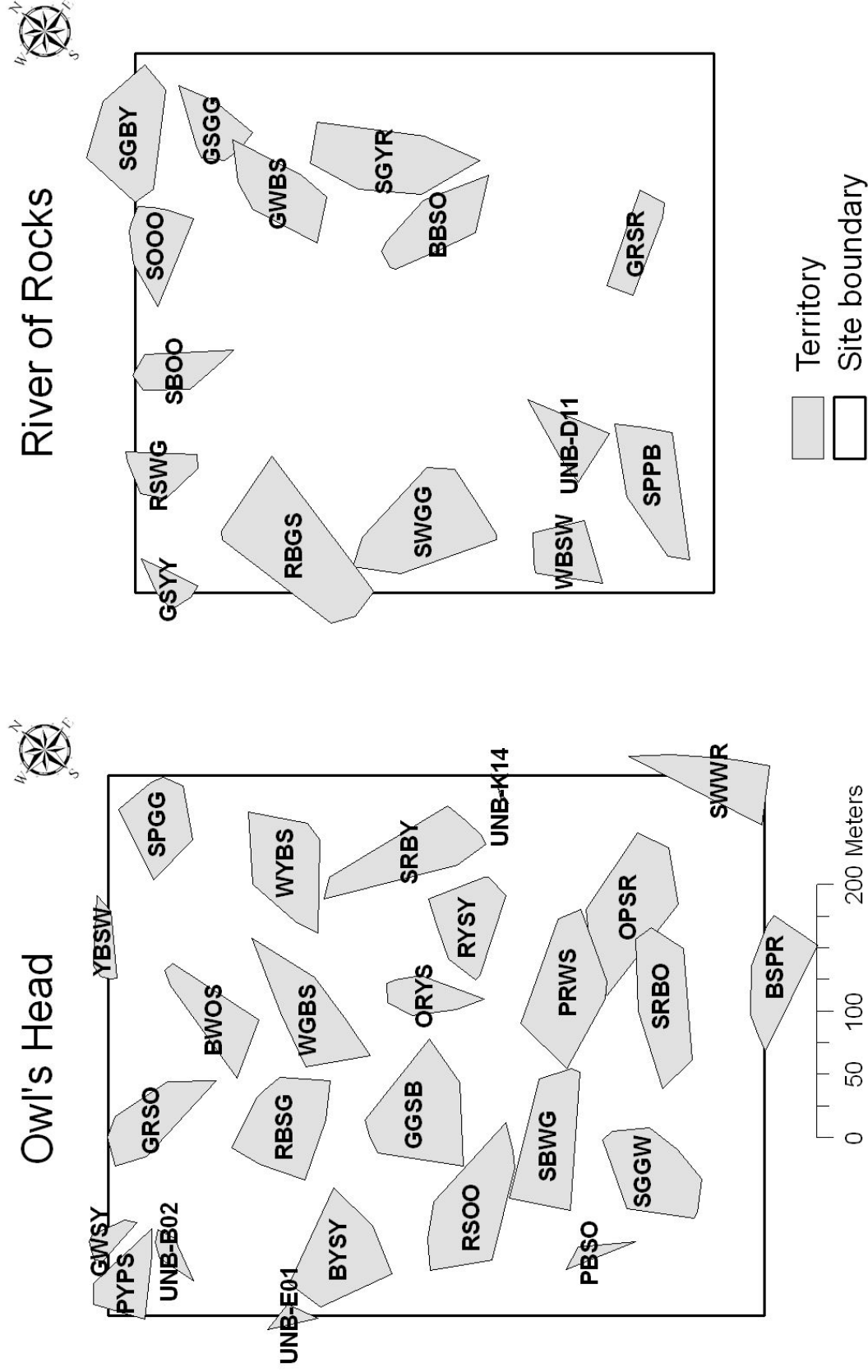
Territories defended by birds at Owl's Head and River of Rocks sites during the 2003 season.
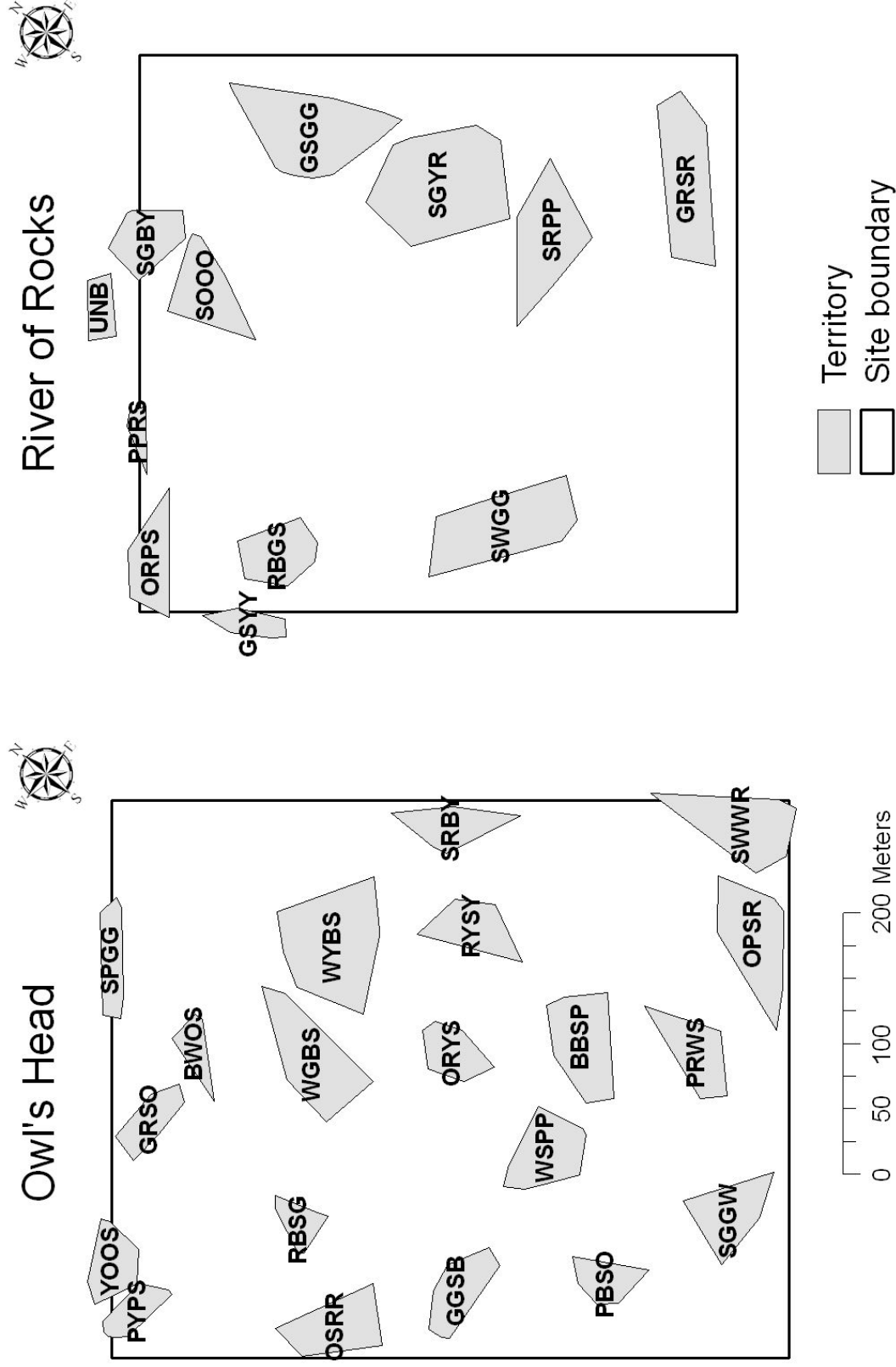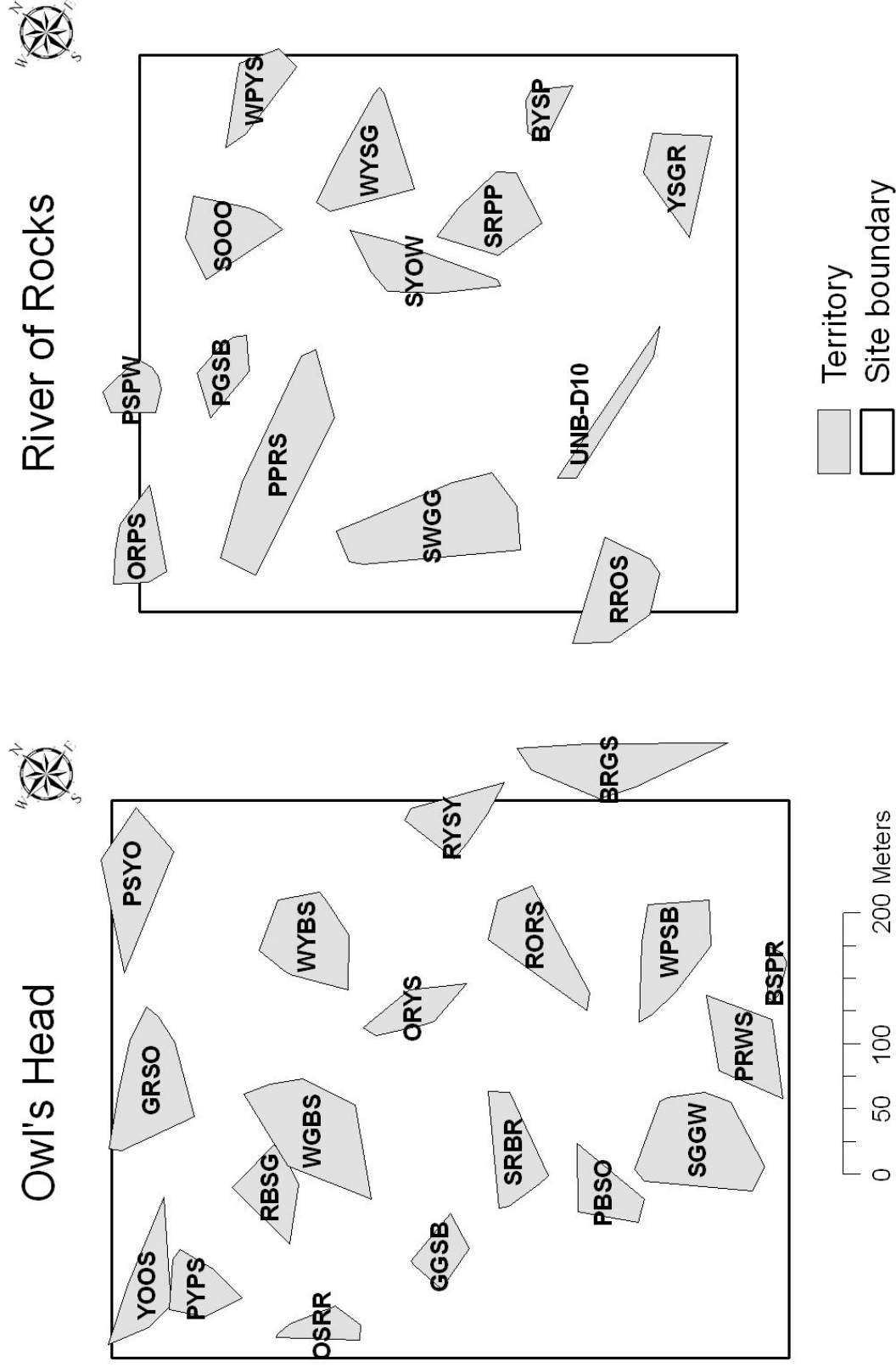

Owl's Head

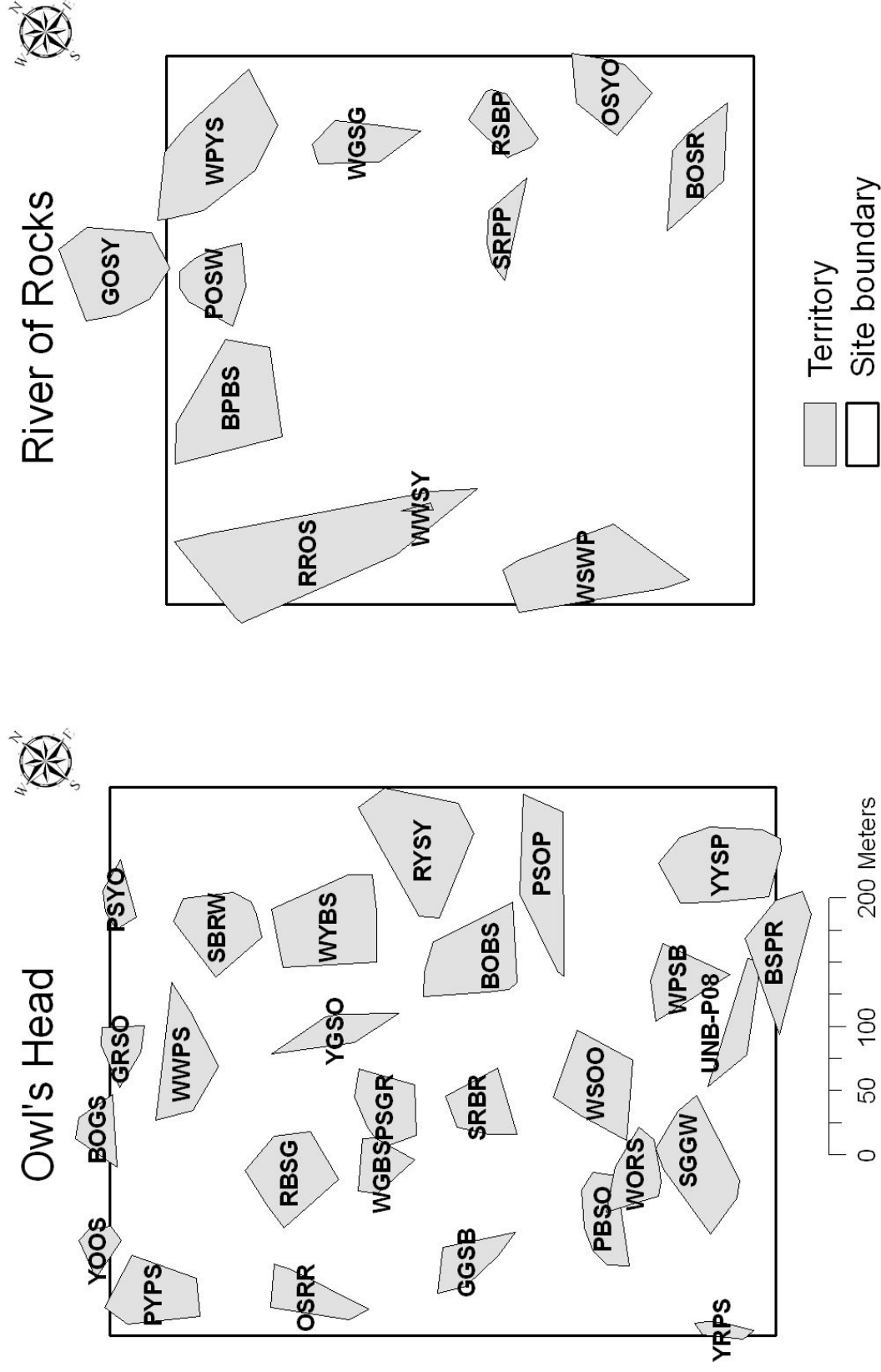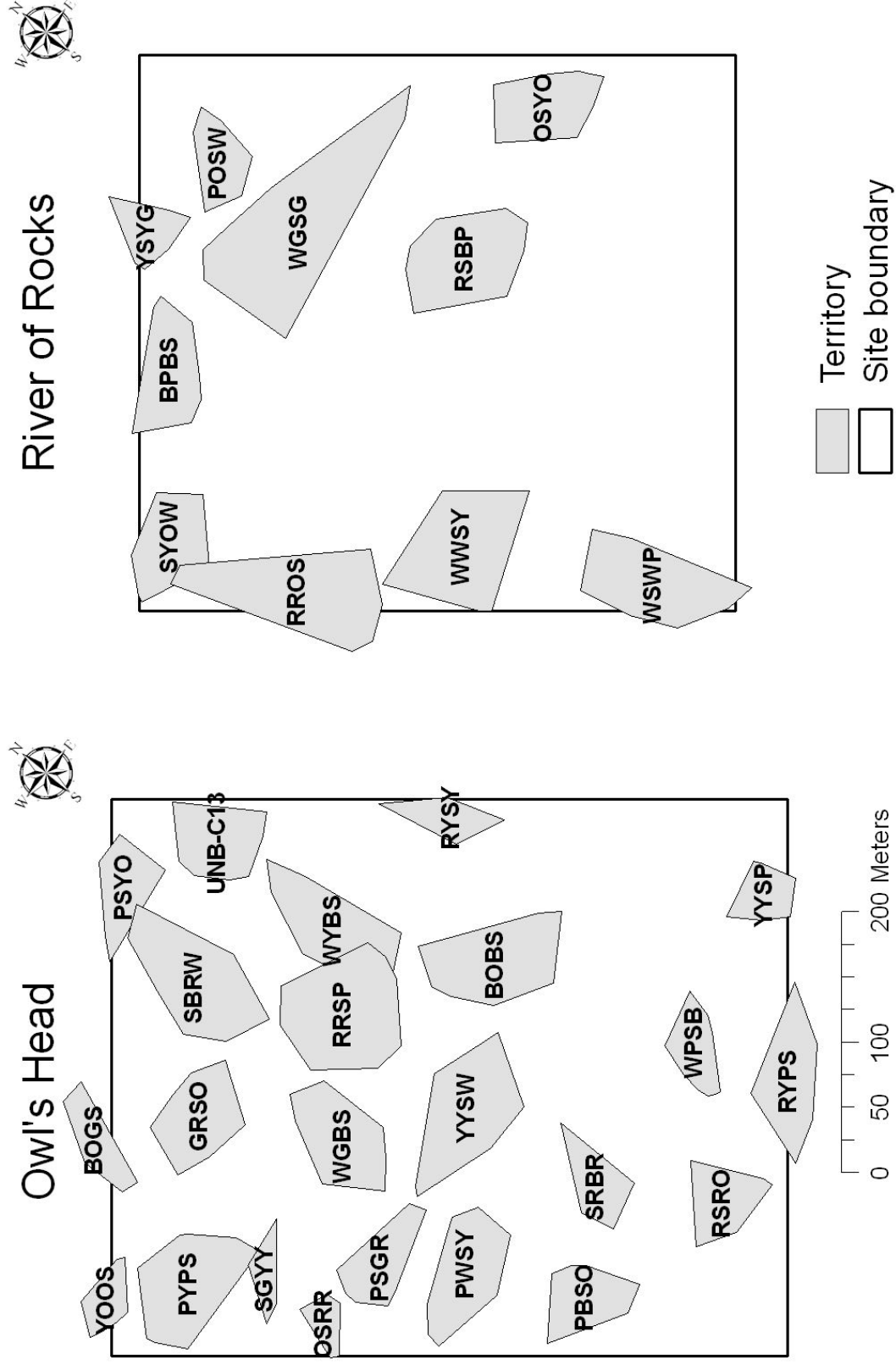River of Rocks

Territory
Site boundary
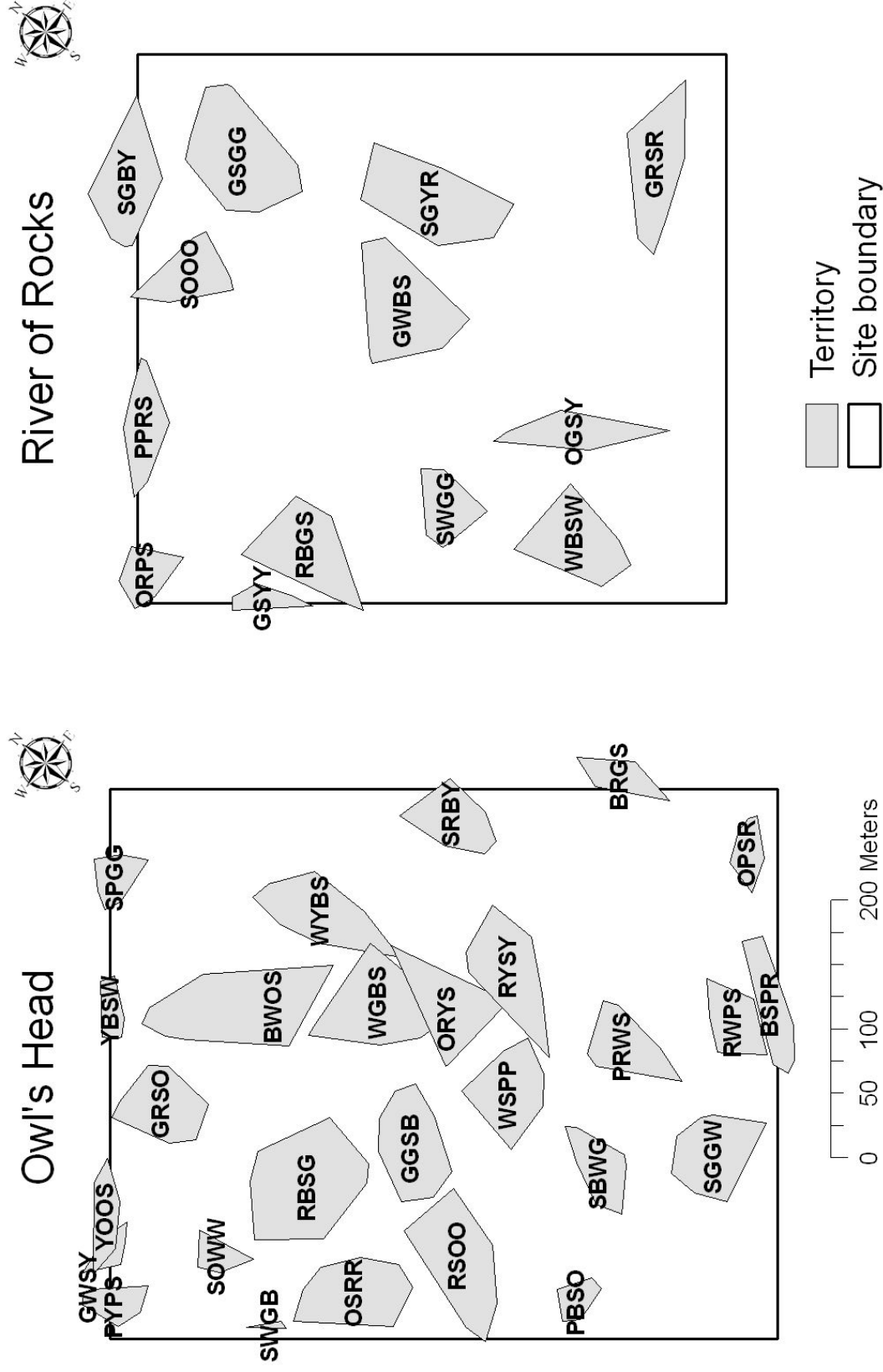
Territories defended by birds at Owl's Head and River of Rocks sites during the 2004 season.

Territories defended by birds at Owl's Head and River of Rocks sites during the 2005 season.
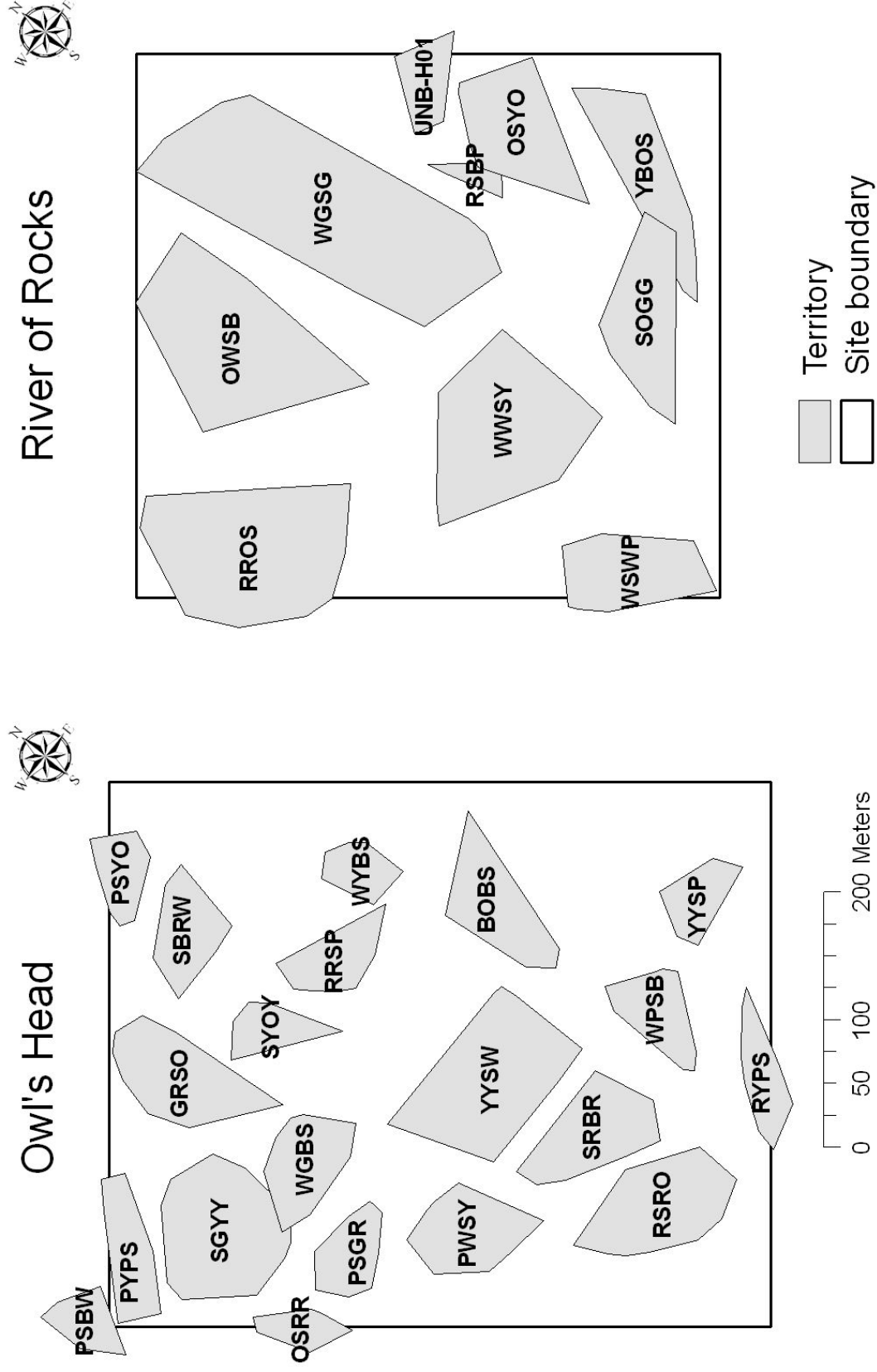
River of Rocks

Owl's Head

0   50   100   200 Meters

Territory

Site boundary

Territories defined by birds at Owl's Head and River of Rocks sites during the 2006 season.

River of Rocks

Owl's Head

Territory

Site boundary

0   50   100   150   200 Meters

Territories defended by birds at Owl's Head and River of Rocks sites during the 2007 season.

Owl's Head

River of Rocks

Territory
Site boundary

0   50   100   200 Meters

Territories defended by birds at Owl's Head and River of Rocks sites during the 2008 season.

River of Rocks

Owl's Head

Territory
Site boundary

0   50   100   200 Meters

Territories defended by birds at Owl's Head and River of Rocks sites during the 2009 season.

Owl's Head

River of Rocks

Territory

Site boundary